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Analyse écophysiologique et modélisation de l'interaction génotype x environnement x itinéraire technique chez le cotonnier (Gossypium hirsutum L.) au Cameroun pour la conception d'idéotypes

Soutenue le 10 juin 2015 devant le jury composé de

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« Tous les hommes pensent que le bonheur réside au sommet de la montagne alors qu'il se trouve dans la façon de la gravir» **孔夫子**

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Lorsqu'on travaille sur les interactions génotype x environnement, on s'attend à interagir avec de nombreuses personnes, ce fut bien le cas ! Ce travail est donc le fruit d'une réflexion nourrie par de très nombreux échanges. Aussi je tiens à exprimer ma gratitude envers tous ceux que je n'ai pas nommés mais qui m'ont gentiment aidé. Si j'en suis là maintenant c'est grâce à vous tous ! Merci pour la balade, je n'oublierai pas !

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Thesis abstract

Cotton lint is the first natural fiber used in the world. Cotton provides income to more than 10 million persons in West and Central Africa. In Cameroon, it is produced under rainfed conditions and water shortage is the major abiotic factor limiting yield and lint quality. In this context, a breeding program was initiated in 1950 by IRCT (Institut de Recherches du Coton et des Textiles Exotiques) to increase lint yield, fiber quality and disease resistance. After 60 years, this program has released more than 20 cultivars. However, seed cotton yield has been levelling off for more than thirty years. This study analyzed growth and development of main cultivars released from 1950 to 2009 to evaluate genetic gain including drought adaptation traits indirectly bred for. It also analyzed genotype by environment by crop management interactions (GEI) under water limited conditions in order to use a cotton simulation model in Cameroonian conditions. Then, crop simulation model was used to design cotton ideotypes under Cameroonian cropping conditions. An application of this work was in identifying the measurements of key drought adaptation traits to breed for in order to create cultivars that better withstand water stress. Firstly, phenotype evolution over breeding time and its interaction with cropping conditions in Cameroon was evaluated on cotton development, growth (including roots), yield, and fiber quality. Ten major cultivars were studied under rainfed conditions (field) and controlled conditions (greenhouse and phytotron). Classical GEI analysis of variance of cultivars and regression over their respective year of release were done. The results showed that the breeding program succeeded in improving cotton lint yield and the potential of fiber quality when the crop reached physiological maturity before the end of the rainy season. In late season drought, breeding reduced the fiber quality (fiber length, uniformity and strength). Most of the development and growth variables did not change with time, except the number of leaves which reduced. Breeding created cultivars with better potential fiber production and quality, but with reduced plasticity to sub-optimal environments and access to soil water. Secondly, an analysis of GEI for ecophysiological traits conferring a good response to drought was done in good and water limited conditions for a subset of four cultivars. The results indicated that water deficit had a negative impact on almost all plant functions, both under field and controlled environments. The recent cultivar L484 bred for the driest production area had the fastest development, thickest leaves with most chlorophyll and thus maintained the highest level of photosynthesis and transpiration per unit of leaf area in water-limited conditions. In these conditions, L484 had the highest radiation use efficiency and water use efficiency maintenances. Despite these traits this cultivar did not show any improvement in terms of biomass, harvest index and cotton yield across water conditions. Cotton breeding program in Cameroon succeeded in providing a cultivar (L484) better adapted to local conditions, with a higher stability and faster development coupled with a strategy of growth maintenance, without any improvement in yield. Thirdly, the crop simulation model DSSAT CROPGRO-Cotton was used in order to design ideotypes with higher yield than existing cultivars. Field experiments in Cameroon were used to constitute the minimum dataset for the crop model calibration. Forty-two virtual cultivars were generated by increasing or decreasing by 20% from genetic parameters values of cultivar L484 on phenology, photosynthesis, and leaf morphology. Then, cultivars AC, L484 and these virtual cultivars were compared across 99 years of generated weather from WGEN model in two locations. Compared to L484, the cotton ideotypes in Cameroonian rainfed conditions had reduced emergence to anthesis duration, longer reproductive duration, higher level of photosynthesis maximum with thicker leaves, and smaller leaves for Far North region or bigger ones for North region.

Résumé de la thèse

La fibre de coton est la première fibre naturelle utilisée dans le monde. Le coton fournit un revenu à plus de 10 millions de personnes en Afrique occidentale et centrale. Au Cameroun, il est produit exclusivement en conditions pluviales et le manque d'eau est le principal facteur abiotique limitant le rendement et la qualité de la fibre. Dans ce contexte, un programme de sélection a été initié en 1950 par l'IRCT (Institut de Recherches du Coton et des Textiles Exotiques) avec l'objectif d'augmenter le rendement, la qualité de la fibre et la résistance aux maladies. En 60 ans, plus de 20 cultivars ont été créés. Cependant, depuis une trentaine d'année, un plafonnement du rendement en coton graine est constaté. Cette étude a analysé la croissance et le développement des principaux cultivars vulgarisés de 1950 à 2009, pour évaluer le progrès génétique, y compris celui de caractères d'adaptation au stress hydrique indirectement sélectionnés. Elle a analysé les interactions génotype x environnement x pratiques culturales (GEI) dans des conditions hydriques limitantes afin de pouvoir utiliser un modèle de simulation de la croissance du cotonnier. En utilisant ce dernier, les rendements ont pu être prédits et des idéotypes pour les conditions de culture du coton au Cameroun ont été conçus. Une application de ces travaux a été d'identifier les mesures au champ des caractères d'adaptation au stress hydrique pour aider les sélectionneurs à choisir les cultivars qui résistent mieux au stress hydrique. Dans un premier temps, le progrès génétique et son interaction avec les conditions de culture au Cameroun ont été évalués au champ et en milieux contrôlés sur le développement du coton, la croissance (y compris racinaire), le rendement et la qualité de la fibre. Les résultats ont montré que la sélection a réussi à améliorer le potentiel de rendement et de qualité de la fibre lorsque la culture atteint la maturité physiologique, avant la fin de la saison des pluies. Cependant, lors de stress hydrique de fin de cycle, le programme de sélection a réduit la qualité de la fibre. La plupart des variables de développement et de croissance n'ont pas changé avec le temps, sauf le nombre de feuilles qui a été réduit. La sélection a créé des cultivars avec un meilleur potentiel de production et de qualité de fibres mais en perdant en plasticité en conditions sub-optimales et n'a pas amélioré l'accès à l'eau du sol. Dans un second temps, les analyses des GEI des caractères d'adaptation à la sécheresse ont montré que le déficit en eau a un impact négatif sur presque toutes les fonctions de la plante, à la fois au champ et en milieux contrôlés. Le cultivar récent L484, créé pour la zone de production la plus sèche, a maintenu le plus haut niveau de photosynthèse et de transpiration par unité de surface foliaire dans les conditions défavorables, maintenant ainsi le plus haut niveau d'efficience d'utilisation du rayonnement et de l'eau. Cependant, cela n'a pas permis d'améliorer la biomasse, l'indice de récolte et le rendement de ce cultivar en conditions hydriques limitantes. Le programme de sélection du coton au Cameroun a réussi à fournir un cultivar (L484) mieux adapté aux conditions locales, avec une plus grande stabilité et un développement plus rapide, mais sans aucune augmentation de rendement. Dans un dernier temps, le modèle de simulation de la croissance du cotonnier, DSSAT CROPGRO-Cotton, a été utilisé afin de définir les idéotypes conduisant aux rendements les plus élevés. Des expériences de terrain au Cameroun ont été utilisées pour constituer l'ensemble de données minimum pour l'étalonnage du modèle. Quarante-deux cultivars virtuels ont été générés par des modifications de ±20% par rapport aux valeurs de 5 paramètres génétiques du cultivar L484 (phénologie, photosynthèse et morphologie des feuilles). Les cultivars AC, L484 et les quarante-deux cultivars virtuels ont été comparés dans 99 années de temps généré par le modèle WGEN en deux lieux. Par rapport à L484, les idéotypes avaient une durée réduite entre levée et floraison et plus longue de phase reproductive, un plus haut niveau de photosynthèse maximum avec des feuilles plus épaisses, et des feuilles plus petites pour la région de l'Extrême Nord ou plus grandes pour la région du Nord.

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List of abbreviations

Ψ_{PD}	Predawn leaf water potential
+b	Yellowness index
$\sum PAR_{int}$	Total intercepted photosynthetically active radiation
A	CO2 assimilation rate
A1239	Cultivar IRMA A1239
A333	Cultivar Allen 333-57
AC	Cultivar Allen Commun
AÏDA	Agroécologie et intensification durable des cutlures annuelles
AMMI	Additive main effects and multiplicative interaction
CEC	Cation exchange capacity
CICAM	Cotonnière Industrielle du Cameroun
CIRAD	Centre de coopération internationale en recherche agronomique pour le dévelopement
CMG	Crop management group
conv	Conversion factor for root studies
CSDL	Critical short day length
CSIRO	Commonwealth Scientific and Industrial Research Organisation
CSM	Crop Simulation Model
D742	Cultivar IRMA D742
DAP	Days after planting
DSSAT	Decision Support System for Agrotechnology Transfer
E	Environment
EM-FL	Duration from emergence to flowering
ET_a/ET_m	Actual to maximum evapotranspiration
EUW	Effective use of water
FAO	Food and Agriculture Organization of the United Nations
FL-LF	Duration from 1st flower to end of leaf expansion
FL-SD	Duration from 1st flower to 1st seed
FL-SH	Duration from 1st flower to 1st pod
FTSW	Fraction of soil transpirable water
G	Genotype
GDD	Growing degree days in base 13°C
GEI	Genotype x Environment Interaction
GGE	Genotype + Genotype x Environment Interaction
GH2O	stomatal conductance
GMO	Genetically modified organism
HVI	High volume instruments
IR1243	Cultivar IRMA 1243
IR9697	Cultivar IRMA 96+97
IRAD	(Institut de Recherche Agricole pour le Développemen
IRCO	Cultivar IRCO 5028

IRCT	Institut de Recherches du Coton et des Textiles exotiques
k	Light interception coefficient
L457	Cultivar IRMA L457
L484	Cultivar IRMA L484
LAI	Leaf area index
LFMAX	Maximum leaf photosynthesis rate at 30°C, 350 vpm CO2 and high light
LTC	Natural Fiber Technology and Characterization Laboratory
LVL	Length of leaf vein localized on the left to the central vein of the upper side
max d	Maximum distance for water or nutrient migration in the soil to the root
N1BF	Node of insertion of the first fruiting branch
NASA	National Aeronautics and Space Administration
NAWF	Number of nodes above the white flower on 1st position on the fruiting branch
NKOUR	Cultivar N'Kourala
ns	non significant
PCA	Principal component analysis
PODUR	Time required for cultivar to reach pod load under optimal conditions
PRER	Potential root extraction ratio
PROBE-W	PROgramme de Bilan de l'Eau du sol
RD	Average distance between roots
Rd	Brightness index
R-ETP	Rainfall - potential evapotranspiration
RI	Relative importance
RLD	Root length density
RMSE	Root mean square error
RRMSE	Relative root mean square error
RUE	Radiation Use Efficiency
RWUMX	Maximum uptake per unit root length
RWUP1	Potential root water uptake to potential evapotranspiration threshold for leaf expansion
SD	Standard deviation
SD-PM	Duration from 1^{st} seed to 1^{st} open boll
SFDUR	Seed filling duration
SIBAGHE	Systèmes intégrés en biologie, agronomie, géosciences, hydrosciences, environnement
SIZLF	Maximum size of full leaf
SLA	Specific leaf area
SLAVR	specific leaf area under standard growth conditions
SLW	Specific leaf weight
Sodecoton	Société de développement du coton Camerounais
SSA	Sub Saharan Africa
THRSH	Threshing ratio
TSLA	Plant total synthetized leaf area
UHML	Upper half mean length
UMR	Unité mixte de recherche
UPR	Unité propre de recherche

VC	Virtual cultivar
WS	Water status
WUE	Water use efficiency
XFRT	Maximum biomass allocation to reproductive organ
XSWFAC	Potential root water uptake to potential evapotranspiration threshold for photosynthesis and allocation to growth organs
YR	Year of release
$\varepsilon_a$max	Maximum value of light interception that can be attained by the crop

Introduction

1. Economic importance and plant description

1.1. Economic importance of cotton

Cotton belongs to the *Malvaceae* family and *Gossypium* genus. Only four species are cultivated for their fibers: two diploid genomes, *arboretum* and *herbaceum*, and two tetraploid genomes, *hirsutum* and *barbadense*. Cotton fiber is the first naturel fiber used in the world (Park et al., 2012), mainly for textiles and clothing. On average for the period between 1993 and 2013, main cotton fiber producing countries were China, the USA and India with 5.5, 3.9 and 3.0 million tons, respectively (FAO Stats, 2015). In West and Central Africa, cotton is an important cash crop which provides income for more than 10 million people (Baffes, 2004). Ninety percent of commercial cotton fibers come from upland cotton (*Gossypium hirsutum* L) (CIRAD, 2003). In this study we will focus on upland cotton. In discussing its production and other aspects, we will refer to cotton fiber, cotton seed and seed cotton (cotton fiber + cotton seed).

1.2. Morphology of cotton and its description variables

Cotton is a perennial shrub which is cultivated as an annual crop, whose plants are destroyed after harvesting the seed cotton. Cotton is composed of vegetative parts (the leaves, the stem and the roots), and of reproductive parts (the squares, the flower, and the bolls). The leaves and the roots are the source organs. The leaves provide carbon to the plant, via photosynthesis, transforming the light into energy and carbon dioxide into sugars. The roots provide water and nutrients. The stems and petiole are linking organs; they allow these nutrients, sugar, and water to flow from organs to others. The reproductive organs are the main sink organs where the products of photosynthesis are accumulated.

1.2.1. Vegetative compartment

1.2.1.1. Aerial compartments

Leaf compartment

The leaves are broad and lobed, with three to five lobes (Figure 1). Each leaf is represented by an area and a dry weight. Each leaf contains stomata, sometimes open or close, these are the main "doors" for gas exchanges (carbon dioxide, dioxygen, water) with the atmosphere. The leaves contain hair and their pilosity range from no hair to very hairy. The leaf compartment is composed of all leaves. It is described with its total area (sum over all leaves areas) or with its leaf area index (LAI: ratio of plant total area of leaves to its ground area occupation); and by its relative thickness

expressed by the specific leaf area (SLA: ratio of leaf area to its leaf dry weight). The leaf compartment concentrates almost all the photosynthesis process. This process consists in intercepting light, transforming it into energy and using the energy to turn carbon dioxide and water into dioxygen and sugars.

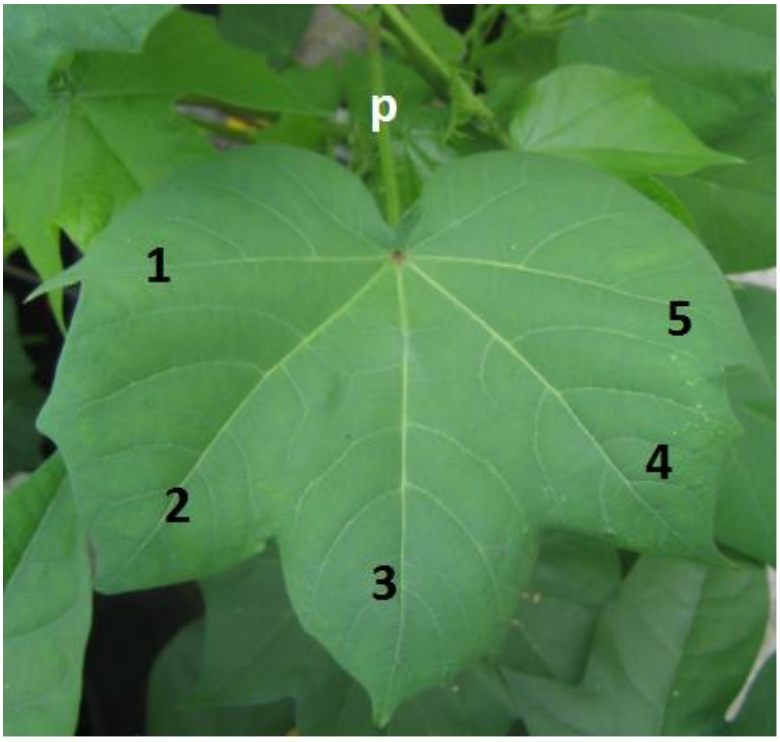

Figure 1. Picture of the upper side of a cotton leaf.
Each number is associated with each lobe. This leaf has 5 lobes as indicated by the 5 main veins running from the petiole (indicated by the white letter p; it connects the leaf to the stem) to the extremity of each lobe. Picture taken in a greenhouse at CIRAD, Montpellier, France, 2012. *R.Loison*

Key variables for the characterization of the cotton leaf compartment are listed in what follows. The evaluation of LAI is important; it defines how much light cotton can intercept at a point in time. It is considered that above a LAI of 3, approximately 95% of light is intercepted. Figure 2 shows closed canopy (Figure 2a, all light intercepted) and developing canopy with reduced light interception (Figure 2b). Likewise, evaluation of SLA is important; as an indirect indicator of chlorophyll content. It defines how efficiently intercepted light can be transformed into sugar. Nonetheless, as mentioned earlier, photosynthesis needs water and carbon dioxide. Since gas exchanges are of first interest, stomatal conductivity, carbon dioxide assimilation rate are also important indicators of the efficiency of transformation of light into sugars. The radiation use efficiency (RUE) of cotton is defined as its total dry biomass divided by its sum of intercepted light.

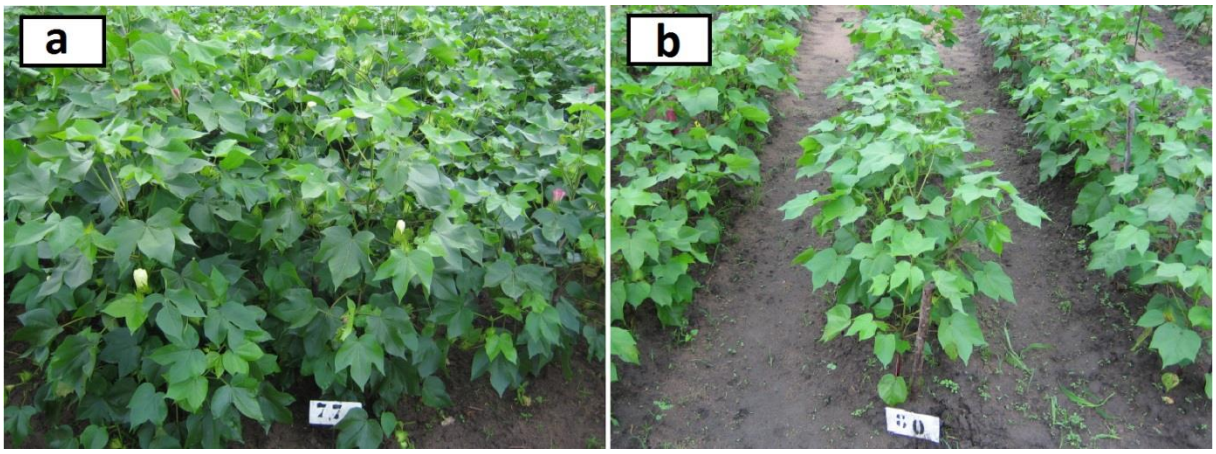

Figure 2. Picture of three lines of cotton plants in field experiment of Sanguéré, Cameroon, 2012.
Figure 2a represents a closed canopy at 84 days after planting, in early planting conditions for cultivar IRMA L457 released in 2009; leaves are touching each other, and all sunlight is intercepted. Figure 2b represents a canopy which is not intercepting all sunlight yet at 57 days after planting in late planting conditions for cultivar Allen Commun released in 1950. *R.Loison*

Stem compartment

The main stem is composed of nodes and internodes connecting each node to the other. On each node there is a leaf and an axial bud. The first node emitted on the main stem is the cotyledon node (Figure 3). For each of the first nodes above, there is either no branch or one vegetative branch (Figure 3). A vegetative branch does not carry any fruit but can emit secondary branches that carry fruits (Goldsworthy and Fisher, 1984). After a few nodes on the main stem, the first fruiting branch is emitted (Goldsworthy and Fisher, 1984); this node is called node of insertion of the first fruiting branch (N1FB). Above that node, all nodes contain a single fruiting branch (Figure 3). The main stem and the vegetative branches show a continuous (monopodial) development whereas the fruiting branches and the secondary fruiting branches on the vegetative branches show a discontinuous (sympodial) development in a zig zag manner (Figure 3). In addition, cotton shows a 3/8 phyllotaxy (every new branch develops on an axis rotated by 135° compared to the former).

The stem compartment is characterized by its number of nodes on the main stem, its average length of the internodes on the main stem, its main stem height, its number of developed vegetative branches, its number of fruiting branches, its duration between the sequential emergence of nodes on the main stem (defined here as the phyllochron), and its biomass.

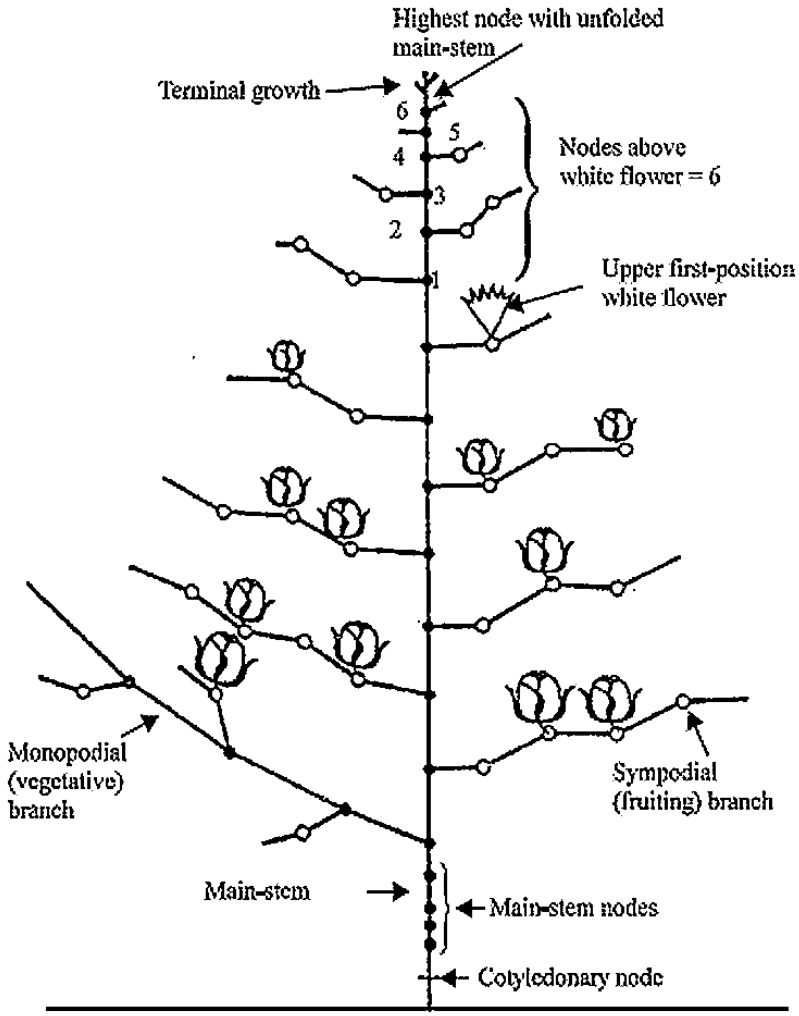

Figure 3. Typical cotton plant morphology.
It shows, the cotyledonary node, the 4 upper nodes on the main stem which do not carry any branch, the upper node which has a vegetative branch. That vegetative branch carries a secondary fruiting branch. Finally, on the highest part of the main stem, there are 11 developed fruiting branches. Since six nodes are above the white flower (flower of the day) in first position on the main stem (NAWF=6), cut-out is not reached yet. Source: Oosterhuis et al. (1993)).

1.2.1.2. Root compartment

Cotton has a tap root system. It shows a main root probing down into the soil and secondary roots plugged on that root. This root system is characterized by the depth it reaches in the soil, its total length, its speed of growth, its biomass, and the importance of soil horizontal occupancy defined by the rooting angle made by secondary roots at the top most depths. In situ, root length is often defined relatively over the volume of soil it occupies (root length density (RLD)). In addition, average distance between roots (RD) gives a representation on how well this root length is occupying the soil. Finally, the potential root extraction ratio (PRER) is the combined indicator of root length and soil occupation. It evaluates root potential extraction of water or nutrients present in the volume of soil considered.

1.2.2. Reproductive compartment

The reproductive organs are the squares, the flowers, and the bolls (Figures 4 and 5). The square is the early stage of a reproductive organ before pollination. It has the shape of a triangular pyramid. After 3 weeks, the square shows a candle shape and the anthesis (flowering) is imminent. The flower is perfect (hermaphrodite). In most cases, self-pollination happens but pollinating insects could result in as much as 30% of flower pollination (Meritan et al., 1993). Pollination results in a change of color of the flower, turning from cream to pink. Then, ovary turns into the developing boll. This boll matures for approximately 50 days and then "opens". Opening happens when the carpels (boll wall) dehisce. When open, dried carpels usually show four or five locules, each of them containing seed cotton. In each locule, there are as many seeds as developed ovules. Seed cotton is composed of seeds and fibers attached to it.

Figure 4. Picture of a fruiting branch of cotton bearing a flower of the day (a) and on the next node, a square.
Credits: M. Booghs, greenhouse, CIRAD, Montpellier, France, 2012.

Figure 5. Different stages of reproductive organs of cotton (*Gossypium hirsutum L*).
Early square (a), developed square (b), flower of the day or white flower (c), pollinated flower or pink flower (d), small and young boll to large and mature boll (e to h), opening boll (i), and fully opened boll (j). *Adapted from Harris Barnes Jr.*

The variables characterizing reproductive compartment are of two kinds. The first set of variable describes the quantity of reproductive material; its yield and components. The second set describes the quality of reproductive material.

First, the reproductive compartment is described by a biomass and a relative biomass (% of total aerial plant biomass). When the reproductive biomass is multiplied by the threshing ratio (average mass of seed cotton over the boll mass (carpel + seed cotton)), we obtain the seed cotton yield. Another way to calculate that seed cotton yield is achieved by multiplying the aerial dry biomass (ADB) by the harvest index (HI: ratio of seed cotton mass to the entire plant biomass). Seed cotton yield can be computed by multiplying the number of bolls per hectare by the average seed cotton weight in a boll. The seed cotton yield multiplied by the fiber percentage gives the fiber yield.

Secondly, seeds and fibers are described by their quality. The weight of a hundred seeds is called the seed index or seed mass index (SI). These seeds are also described by their content in protein and in oil. Seed oil is used in human nutrition and cotton seed cake is used in animal feeding. The fibers are mainly made of cellulose (80-90%). They are ranked into different classes of quality according to various factors. This is of economic importance as the quality either results in a bonus or a discount on the cotton fiber price. Cotton fiber has a length (upper half mean length: UHML) and a uniformity index which indicates the ratio of the average length of all fibers to the UHML.

The short fiber index indicates the ratio of fibers shorter than 12.7 mm. Then strength and elongation represent fiber traction force applied to fiber when it breaks and, percentage of extension of the fibers before a break occurs when measuring strength, respectively. The standard fineness of a fiber is another indicator of quality; finer fiber can produce higher quality fabrics. Nonetheless, extremely thin fibers could be immature. Maturity ratio is the percentage of fiber filling. A maturity ratio of 100% corresponds to a fiber with lumen radian equal to fiber wall thickness. Fibers with maturity superior to 80% are considered mature. The percentage of mature fiber is the ratio of mature fibers to all fibers. The micronaire index is an index combining fineness and maturity. Finally, fiber color is estimated by its yellowness (+b) index and brightness index (Rd).

1.3. Growth and development

Cotton is an indeterminate plant since its vegetative and reproductive growths happen at the same time. Competition for nutrients, water and sugars happen between vegetative and reproductive parts. At some point in the cotton cycle, the reproductive parts use almost all the resources and vegetative growth stops until reproductive parts are matured. This stage is called cut-out and is measured by the number of nodes above the white flower on 1st position on the fruiting branch (NAWF, Figure 3). Cut-out happens when NAWF decreases to five.

Cotton development begins with emergence, when both cotyledons are fully expended (Figure 6). Then, the first flower blooms, this is anthesis. Then other flowers bloom and bolls mature. Then, the first fully mature boll opens, followed by all others. The approximate length of all stages described above is found in Table 1.

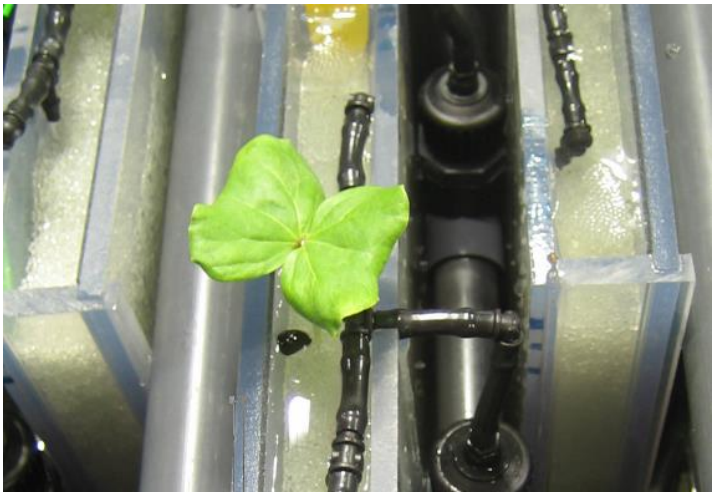

Figure 6. Emergence of cotton plant in hydroponic conditions.
Rhizotron, CIRAD, Montpellier, 2012. One cotton plant has just emerged, both cotyledons have fully expanded.

Table 1. Approximate length in days of main development stages of cotton.

Development stage	Length (days)
Planting-Emergence	6 – 10
Emergence-Anthesis	40 – 60
Anthesis-Cut out	40 – 50
Cut out- 1st open boll	15 – 25
1st open boll- 100% open boll	35 – 55

1.4. Requirements for growth and development of Cotton

1.4.1. Temperature

In non-limiting conditions, the length of each stage is only dependent on the temperature, cotton is not photoperiodic. Cotton is a hot temperature crop but it can be cultivated at any place where there are more than 200 days of temperatures above 0°C, and summer temperature high enough (CIRAD, 2003). As a result, cotton is cultivated from the latitudes 47°N to 32°S. The age of the crop can be calculated as a sum of growing degree days (GDD) with a temperature where cotton stops its growth (basis temperature) of 13°C; as follows:

$$GDD_i = (Tmax_i - Tmin_i)/2 - 13 \qquad \text{Eq.1}$$

$Tmax_i$ and $Tmin_i$ are the maximum and minimum temperatures (in °C) recorded in day i.

For cotton, from planting, emergence takes approximately 35 to 40 GDD, anthesis 530 to 650 GDD, first open boll 1130 to 1300 GDD, and the full cycle, 1450 to 1600 GDD (CIRAD, 2003).

1.4.2. Water

Cotton needs about 500 mm of water during its cropping cycle from planting to at least cut-out. Water deficit will slow or stop growth of vegetative tissues; it can also be the cause of fruit shedding during the first 10 days of each boll where they are the most sensitive. Cotton fiber is reduced by insufficient water supply. Cotton is also sensitive to anoxia when drainage is insufficient.

1.4.3. Solar radiation

Cotton needs a high level of solar radiation. The highest photosynthetic activity happens at solar radiation of 30 MJ/m^2/day. Solar radiation is always limiting for cotton growth and is never optimal. For example, in Mali, during the cropping cycle solar radiations only reach 22 MJ/m^2/day (CIRAD, 2003).

1.4.4. Soil properties

Cotton will perfectly suit homogeneous, deep, well drained, and fertile soils. Fertility should include major nutrients like N, P, and K, but also secondary ones like S and Mg, and micronutrients like B and Zn. Optimum pH for cotton culture range from 6 to 7, and soil should not be too acid (below 5). Cotton is not halophile. Some ecological properties can be influenced by crop management (water, soil properties). Consequently, specific management of cotton crop is important to achieve cotton ecological requirements.

1.5. Cotton cropping management

Cotton is cultivated at all levels of intensification. It can be cultivated with full mechanization, high level of fertilization, on big areas. It can also be cultivated manually, with cattle ploughs, reduced access to fertilizers, on small areas. Cotton is either irrigated or rainfed, on 53% and 47% of the surface cultivated, respectively. In Sub Saharan Africa, cotton is cultivated by smallholders, usually rotated with food crops, so that they can benefit from residual fertilizer after the cotton is harvested.

In the first 6 weeks of its cycle, cotton, is very sensitive to weeds. In highly intensified systems, where genetically modified cultivars which are resistant to herbicides are used, weeds are controlled by spraying herbicides. In low intensification systems, weeding is usually manually done with a hand hoe.

Pests and diseases also need to be controlled. Once again, it depends on the level of intensification. In Sub Saharan Africa, with low level of intensification, diseases can be controlled with resistant cultivars, whereas pests can be controlled with pesticide applications.

For each condition, cotton cultivars belong to a specific ecotype. In the same ecotype, cotton cultivars show similar pattern. For example, in the production area of the US cotton belt, cotton are short and compact so that they can be harvested mechanically, they have a very high level of production under irrigation and high level of fertilization. In contrast, in Sub Saharan Africa (SSA), irrigation is not possible and fertilizer use is not as easily implemented. Cultivars used in this ecotype are more likely to sustain suboptimal conditions and show a high level of compensation. They are taller than the US ecotype and are suitable for manual harvesting.

Management of the crop depends on its ecotype. In SSA where cotton is mainly rain-fed, planting date is tremendously important. A planting date delayed by 10 days reduces potential seed cotton yield by 350 kg/ha compared to optimal planting date (CIRAD, 2003). Indeed, non-favorable

late planting dates desynchronize cotton cycle with the rainy season, and water stress is likely to impact on cotton morpho-physiological traits.

2. Effects of water stress on cotton morpho-physiological traits

Water deficit has a negative impact on almost all the plant functions (Hsiao, 1973). Overall stomatal closure and transpiration reduction in response to water deficiency have long been established (Hsiao, 1973). Sadras and Milroy (1996) reviewed the main crops physiological responses to drought. The first trait reduced in water stress conditions is leaf expansion (Constable and Hearn, 1981; Rosenthal et al., 1987) and when drought becomes more severe, photosynthesis (Ackerson et al., 1977; Chastain et al., 2014), transpiration (Rosenthal et al., 1987), evapotranspiration (Tardieu and Davies, 1993), transpiration efficiency (Li et al., 2012), stomatal conductance (Chastain et al., 2014; Loka and Oosterhuis, 2014; Shimshi and Marani, 1971) are also affected. As a consequence, drought increases specific leaf weight (da Costa and Cothren, 2011). Chlorophyll content could be increased (da Costa and Cothren, 2011) or decreased (Li et al., 2012) by drought. Net photosynthesis is primarily limited in drought conditions by increase in respiratory and photorespiratory carbon losses (Chastain et al., 2014), not inhibition or down-regulation of electron transport through photosystem II (Chastain et al., 2014).

In addition to physiological traits, water stress also reduces phenotypic traits. Papastylianou and Argyrokastritis (2014) found a smaller total leaf area, smaller aerial biomass compared to optimal conditions. Water deficit inhibits the growth of leaves, petioles, and branches, but does not inhibit growth of the stem (Fernandez et al., 1996). In drought conditions, cotton reduces its roots biomass (Zhang et al., 2013). Exposure to water deficit decreases the shoot to root ratio through a more pronounced inhibition of shoot growth (Fernandez et al., 1996) compared to root growth.

Water deficit inhibits total biomass accumulation and its partitioning in cotton (Fernandez et al., 1996) resulting in increased harvest index (da Costa and Cothren, 2011). Nord and Lynch (2009) found that water deficit generally reduces yield. Many of the yield components, plant mapping, and biomass parameters are affected by drought (da Costa and Cothren, 2011). However, Papastylianou and Argyrokastritis (2014) found that the ginning out-turn is not affected by water deficit.

Timing of stress event is critical for cotton yield (Snowden et al., 2014). Drought stress during squaring results in significantly shorter plants with fewer nodes; however, with same yield (Snowden et al., 2014) if cotton has sufficient time for regrowth. The early flowering growth stage is

the most sensitive to drought stress and produces the lowest yields, the lowest fruit retention, and poor fiber quality (Snowden et al., 2014). Drought events at peak bloom results in similar yield losses to those at squaring, but poorer fiber quality (Snowden et al., 2014).

Drought also impacts negatively on fiber quality. Indeed, insufficient water supply decreases fiber length and uniformity, and increases short fiber content (Feng et al., 2014). It also decreases fineness, maturity ratio and subsequently micronaire (Feng et al., 2014).

Padmalatha et al (2012) showed that drought has relatively less impact on fiber initiation but has profound effect on fiber elongation by down-regulating important genes involved in cell wall loosening and expansion process. Nonetheless, significant genotypic differences exist in the relationships of crop water stress index and fraction of transpirable soil water (Lacape et al., 1998). Consequently, response of cotton to water stress depends on the cultivar used. The relation of cotton to water depends on the type of soil, weather conditions, crop management, cultivar used and the context of production.

3. Context of cotton production in northern Cameroon

3.1. Economics

As a typical smallholder cash crop in Cameroon, each year for the last decade, cotton farming provided a global income from 19.5 to 64.9 billion FCFA to more than 240 000 growers and their families (*Source: Sodecoton 2014*). In addition, the cotton industry (agronomy, ginning and oil industries) is a major economic driver in the North and Far North regions. Cameroon produced about 5% of total African lint between 2000 and 2012 (FAOSTAT, 2014).

3.2. Agronomy

In Cameroon, cotton is produced under rainfed conditions (Sultan et al., 2010). Water availability during the crop cycle, characterized by the length and the quality of the rainy season, has a tremendous importance on cotton production (M'Biandoun and Olina, 2006). In addition, other agronomic (soil fertility, pests) and socio-economic (competition between food crops and cotton) factors make cotton a challenging crop to grow in Cameroon. Cotton is planted as soon as the rainy season starts (June or early July). Fertilization application depends on the planting date. In the Northern region, early plantings receive 200 kg/ha of complex fertilizer (NPKSB 22-10-15-5-1) and 50 kg/ha of urea (46%N) at ridging. In the Far North region, early plantings receive the same amount of complex fertilizer, but no urea. In both regions, late plantings less fertilizers (100kg/ha of complex fertilizer and no urea), and after a threshold planting (end of July) they are no longer fertilized.

3.3. Breeding

Each stakeholder in the cotton industry of Cameroon has specific objectives and constraints. Cotton farmers sell their production (seed cotton) to the development company (Sodecoton) and aim at producing a lot of cotton per unit land area. Sodecoton buys the seed cotton from farmers and after ginning, sells the fiber to the international market and the local spinning industry (CICAM). Sodecoton aims at buying a great amount of cotton fiber of high quality to sell to the international market and to meet the specifications of CICAM. Finally, CICAM looks for a compromise between fiber quality and how fast it can be processed as a function of the desired product.

In this context, a breeding program was initiated in Cameroon in 1950 by the IRCT (Institut de Recherches du Coton et des Textiles Exotiques) with the objectives of increasing the fiber yield, the resistance to pests and diseases, and improving the fiber technological characteristics (Levrat, 2010). The breeders are closely working with Sodecoton, and are following their specifications. Breeders breed new cultivars genealogically (pedigree method with self-pollination) using crosses between parental lines both from African (Mali, Cameroon and Ivory Coast) and the USA or other origins. Then from the generation F2 until F4, individual plants are selected, and the self-pollinated seeds of one plant are planted in one line for the next generation. This procedure was repeated for four consecutive years to achieve line stabilization. In the F5 generation, families were selected and thereafter local and multi-local agronomic assessment of the best stabilized lines was performed under rainfed conditions. Plants selected by breeders in the field should not be diseased, should have a minimum number of developed vegetative branches, many large bolls with wide and early opening, moderately hairy leaves, and short internode length. The plants with these characteristics are evaluated in the laboratory. In the laboratory, plants with high ginning out-turn (greater than 42%), and high seed unit mass (greater than 9 g) are selected for extra analysis. Fibers of these plants are analyzed with high volume instruments (HVI). The main criteria evaluated are micronaire, length, strength, maturity, length uniformity, yellow index and reflectance. For lines selected in generation F5, crop earliness and yield on two locations in contrasted ecological zones are also evaluated. Extensive root systems are vital when plants are grown in soils containing insufficient supplies of water or nutrients (Bengough et al., 2011), but comes at carbon costs not consistent with optimizing yield (Eissenstat, 1997). Unfortunately, breeders cannot measure root properties in the field, as it is too labor intensive considering the important number of lines to evaluate. After sixty years of cotton breeding in Cameroon more than 20 cultivars were released (Figure 7).

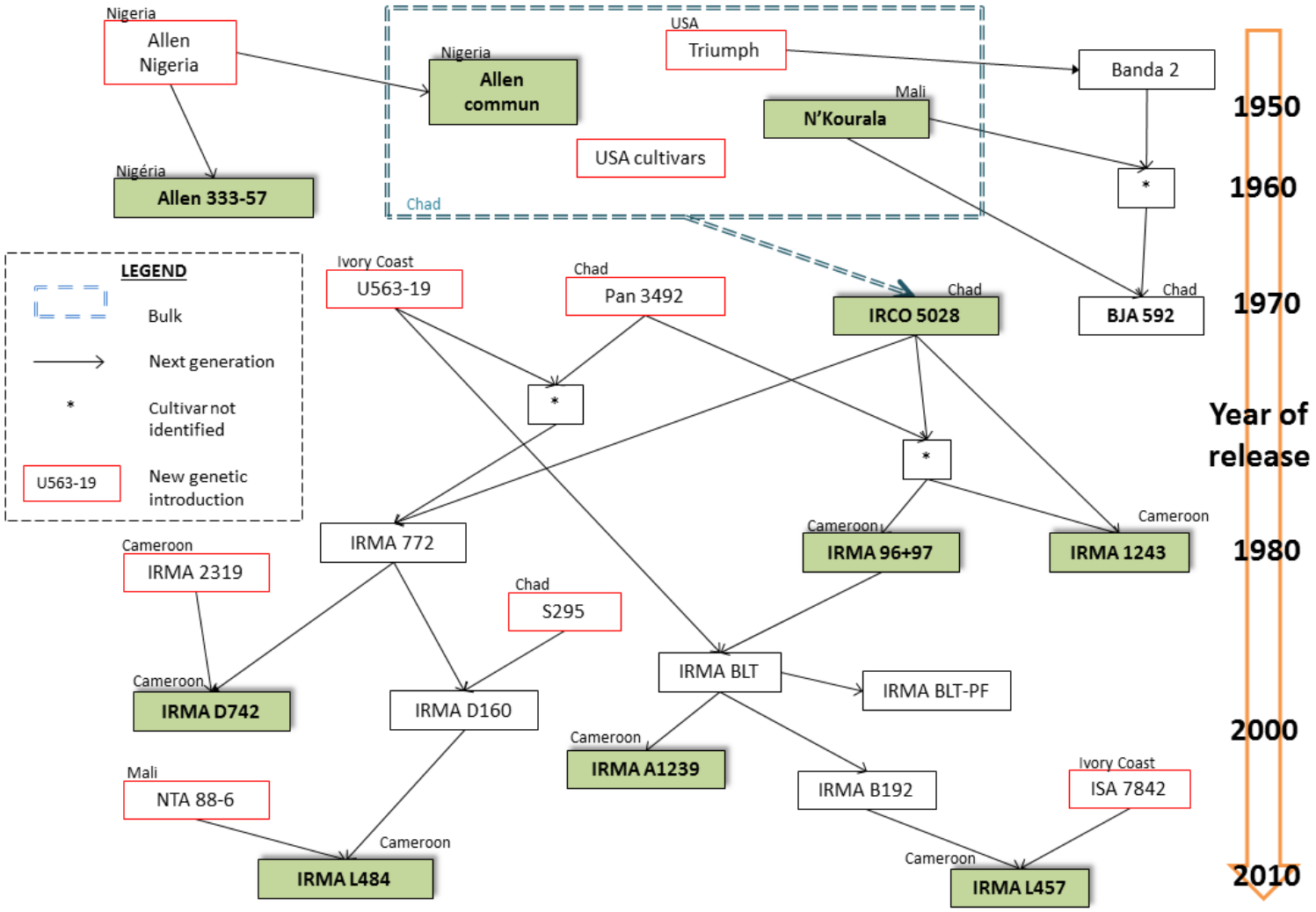

Figure 7. Cameroonian cotton cultivars lineage. Cultivars selected for this study are represented in green. Adapted from M. Booghs Master of Science thesis, 2012.

3.4. Soils

Ngachie (1992), based on FAO-UNESCO soil map analysis, showed that soils in the cotton production area of Cameroon (North and Far North regions) are luvisols (33%), vertisols (19%), regosols (18%), fluvisols (10%), planosols (7%), leptosols (6%), gleysols (5%), arenosols (2%) and ferralsols (<1%). The texture of theses soils range from fine clay, heavy clay, loam, sandy, sandy loam and silty loam (Naudin et al., 2010). Ngachie (1992) described by percentage of occurrence, the major soil fertility constraints in these regions. All soils showed potential to drought stress (100%) due to ustic moisture regime (moisture that is limited but present at a time when conditions are suitable for plant growth). In addition, this author showed low cation exchange capacity (CEC) (38% of the surface), poor drainage (30%), low water holding capacity (25%), alkalinity (25%), erosion hazard (24%), vertic properties (19%), excess of sodium (9%), deficiency in potassium (9%), are shallow (root development limited to first 50 cm of soil) (6%) and salinity (2%). In addition to these structural constraints, soil degradation happens because of non-sustainable agricultural practices (Mahop and Van Ranst, 1997). Mahop and Van Ranst (1997) estimated that 22.5% of the gross margin per hectare resulted from soil degradation in Cameroon.

In Cameroon, soils fertility is an important factor affecting rainfed cotton yield, so is the rainy season pattern.

3.5. Climate: Rainfall analysis in cotton production area of Cameroon

In Cameroon, water shortage is the major abiotic factor limiting cotton yield and lint quality (Leblois et al., 2014; Riaz et al., 2013a). Moreover, climate change models forecast higher risks of droughts (Rizza et al., 2004) and higher variability in rainy season length in arid to semi-arid areas (Vrieling et al., 2013) which will likely cause large yield losses in SSA (Cairns et al., 2012). Northern Cameroon is one region which might be highly affected by climatic change (Cao et al., 2011; Gérardeaux et al., 2013; Leblois et al., 2014). In order to evaluate these issues in this production area, rainfall analyzes were performed in two contrasted cotton growing environments in Cameroon - Far North (Maroua) and North (Garoua) over the period 1979-2004.

In the Far North region, the 80% percentile shows that the ten days rainfall minus the same ten days potential evapotranspiration (R-ETP) was positive on average at least once every five years for the first ten days of June, and for decades from late June to late September (Figure 8). Outside these periods, at least four years out of five, there was a negative balance. The median shows that at least one year out of two, R-ETP balance was positive from the second decade of July until the

first decade of September. The curve of 20% percentile shows that R-ETP was positive on average 4 times every 5 years for the last two decades of August.

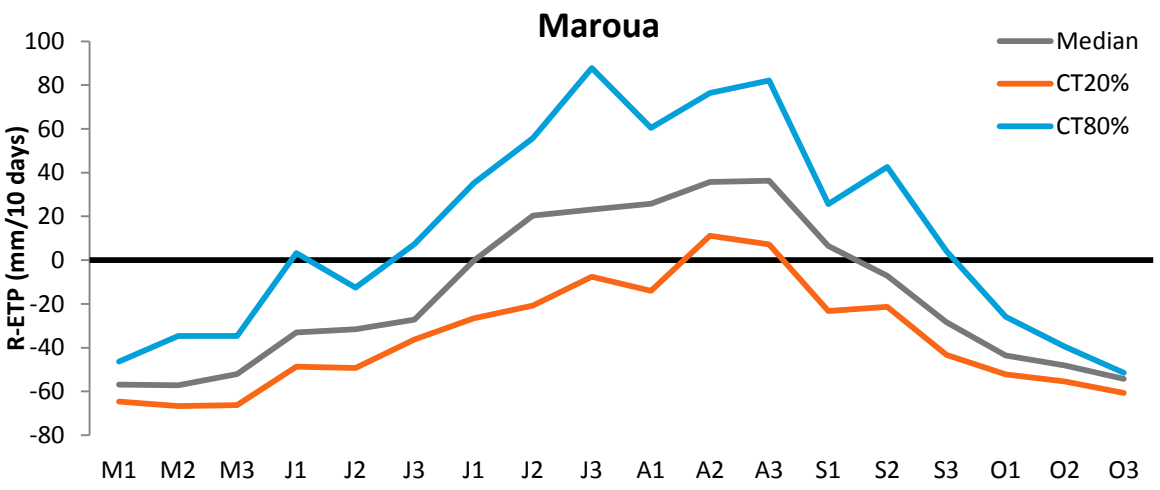

Figure 8. Rainfall analysis in Maroua for 1979-2004.
Rainfall-ETP per decade (in mm) measured between first decade of May (M1) and last decade of October (O3), with a synoptic weather station.

Figure 9 shows that in the North region, the 80% percentile curve shows that R-ETP was positive on average at least once every five years for a longer period of time than in Maroua (last decade of May to early October). The median shows that at least one year out of two, R-ETP balance was positive for a slightly longer (same beginning but later end: second decade of September). Finally, the curve of 20% percentile shows that R-ETP was positive on average 4 times every 5 years only for the first decade of September.

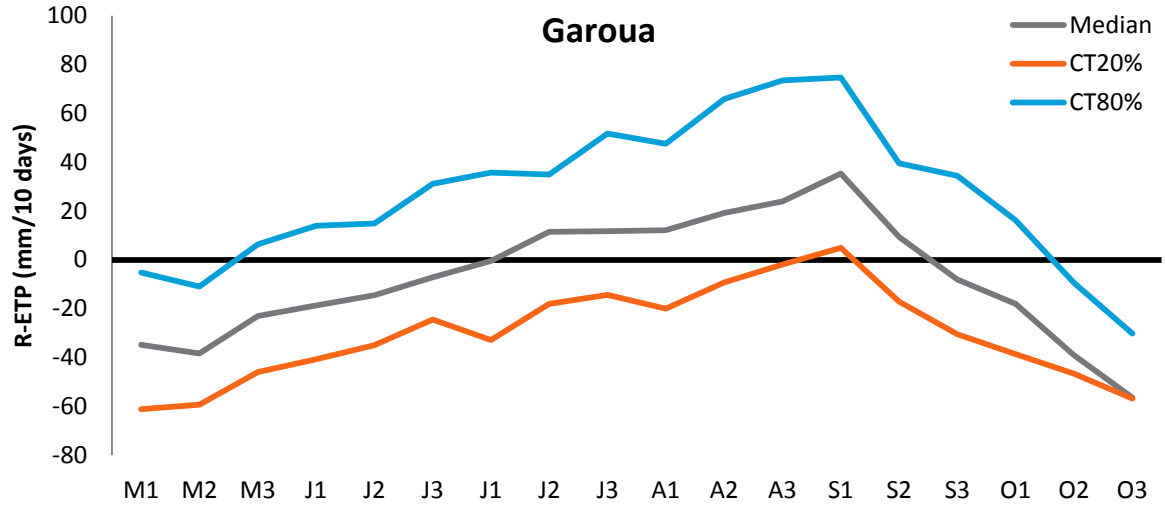

Figure 9. Rainfall analysis in Garoua for 1979-2004.
Rainfall-ETP per decade (in mm) measured between first decade of May (M1) and last decade of October (O3), with a synoptic weather station.

We concluded that drought in the Far North region is mainly due to a short rainy season available for the crop, whereas in the North region, the rainy season is longer and this risk is smaller. Nonetheless, when R-ETP balance is positive, values in Garoua are not as important as in Maroua as showed by y-axis values. As a consequence, North region has a higher risk of moderate and short mid-season drought compared to the Far North region.

In Cameroon, more than 20 cultivars could be cultivated in different rainfed conditions with different dates of planting, facing different water related limitations. In these conditions, Genotype x Environment interaction (GEI) is likely to happen.

4. What is a genotype x environment interaction?

4.1. Generic definition of genotype x environment interaction

Genotype by environment interaction (GEI) can be defined as the differential response of different genotypes under change(s) in the environment (Mather and Caligari, 1976). Figure 10 gives a general description of the evidence of genotype x environment interaction (GEI). There are three levels of interactions: absence (no interaction), presence with change in scale and presence with change in ranking. Figure 10.a shows no interaction. Indeed, genotype green (green) scores 2 points more than genotype red (red) whatever the environment. Environment B increases phenotypes of both genotypes by 1 point. The phenotype of a genotype in an environment can be compute as the fixed effect of the genotype plus fixed effect of the environment. In that case, segments are parallels. Figure 10.b represents GEI with a change in scale. Like in Figure 10.a, green is better than red and environment B is better that A. Nonetheless, the phenotype of a genotype in an environment cannot be compute as the sum of the fixed effects of genotype and environment only. In our example, red is more responsive to environment B than green. Finally, figure 10.c represents a GEI with a cross over. No genotype or environment is better than other one globally. In that case, genotype red is the best in environment A, but it is the worst in environment B.

Generally, when interactions are present, ranking interactions are of main interest for integrative variables (yield, quality) whereas both scale and ranking interactions are important for intermediary variables.

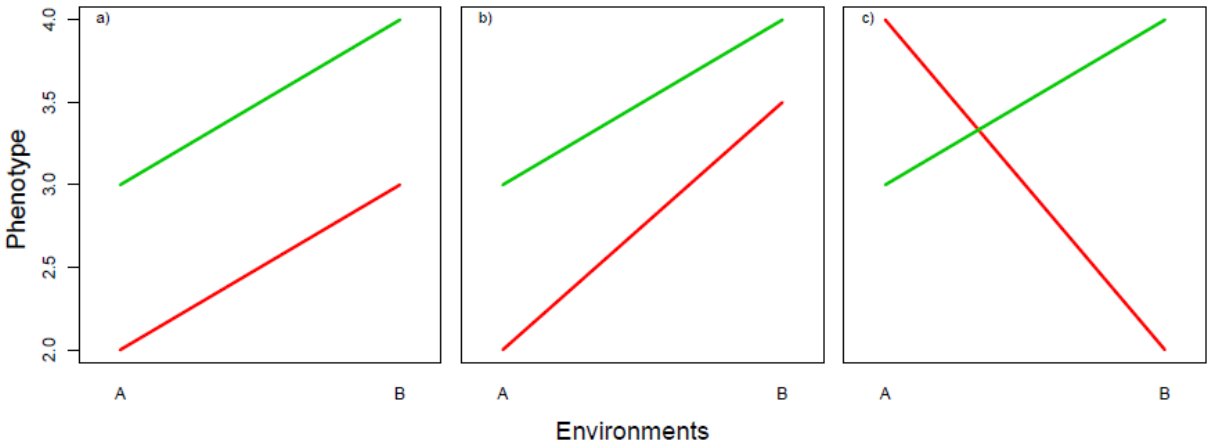

Figure 10. A generic representation of genotype x environment interactions.
Two environments are represented: A and B. Two genotypes are represented with two colors: green and red. a, b, c are the 3 levels of interactions.: a : no interaction; b: moderate interaction with no changes in ranking, c: strong interaction with inversion of ranking.

4.2. Relative importance of genotype, environment and GEI

Campbell et al (2012) described a method for relative importance (RI) of GEI evaluation. The RI was calculated as the ratio of GEI sums of squares to adjusted total sums of squares defined as total sum of squares minus sums of squares of blocks, replications and pooled error.

In a wheat root depth analysis of GEI, Acuna and Wade (2013) showed that genotype main-effects accounted for a RI of 12 %, environment 48 %, and the GEI, 40. In that case, RI of GEI is more than three times more important than genotype RI. Campbell et al (2012) found that for cotton in the USA, environment (E) always had the highest RI, ranging from 43 to 72% and 32 to 80% for yield and its components, and for fiber quality, respectively. They also found that GEI had higher RI compared to genotypes (G) for lint yield (19 and 9%, respectively), yield components (boll m^{-2}, boll weight and seed index) and for fiber quality (length, elongation, uniformity, micronaire and fineness) except for lint percent and fiber strength. In India, seed cotton yield of cotton grown in 12 different environments showed RI of E, GEI and G of 38.5%, 35.3%, and 26.2%, respectively (Riaz et al., 2013b). In that case, environment represented mainly pest incidence (white fly) and all other limiting factors were controlled (irrigation, weeding, and fertilizer application). This could explain why genotype effect shows such a high RI. Some environmental variations are predictable (soil type, soil fertility, plant density etc.) while others are unpredictable (rainfall, temperature, humidity, etc.). Crop management is important to mitigate the impact of these environments. In SSA, impact of unpredictable variation of the environment is important since available management alternatives to withstand sub-optimal conditions are not always available (e.g. no irrigation possible even

if drought experienced). As a consequence, in Africa, environment and GEI usually have high RI, whereas G has small RI. For example, in SSA, bunch yield of bananas showed that RI of E, GEI and G were 58.2%, 33.4%, and 8.4%, respectively (Ortiz, 1998). Likewise, in West and Central Africa, yield of maize showed RI of 85.1%, 11.1%, 3.8% for E, GEI, and G, respectively (Badu-Apraku et al., 2003). Breeding cotton in Cameroon did not succeed in improving yield for decades (Naudin et al., 2010); it is likely that cultivars are not the best options for the range of sub-optimal environments created (pattern of rainy season, soil fertility, planting date, and level of fertilization), GEI should be estimated more precisely. Mechanisms involved in these GEI should be dissected.

4.3. How to analyze G x E interactions?

In this section, several GEI methods are described. First, we review the main statistical methods, describing their pros and cons. Secondly; we describe crop simulation models (CSM), their characteristics and uses.

4.3.1. Statistical model

In this section the principal statistical methods used in GEI studies are described. As reviewed by Acuna and Wade (2013), a range of statistical approaches have been used for the analysis of the GEI. Analysis of variance, regression analysis (Campbell et al., 2012; Finlay and Wilkinson, 1963), nonparametric methods (Fox et al., 1990; Kang, 1991) and pattern analysis of multivariate analytical methods such as the additive main effects and multiplicative interaction (AMMI) model (Zobel et al., 1988), and genotype plus GEI (GGE) biplots (Yan et al., 2000). In AMMI and GGE biplots, the biplots display genotypes and environments on the same plot and are derived from the G and E means.

4.3.1.1. Y: G + E + GEI

The GEI can be analyzed with simple analysis of variance. It includes a fixed effect for the genotype, the environment and a term describes GEI. When significant, there is some GEI. Sometimes, the GEI is partitioned into different sources of variations to distinguish genotype and different environments effects on the global contributions to GEI (Mandel, 1971; Wricke, 1965). The analysis of variance method has the advantage of being simple, it tests and quantifies interaction significance but is global and has no prediction potential (Debaeke and Quilot-Turion, 2014).

4.3.1.2. Regression over environmental index

In this case, each environment is given an index computed as the mean of all genotypes at this specific environment minus grand mean over all environments (Campbell et al., 2012). Then, each genotype is regressed over the range of environmental indexes. Then the slopes and deviation to

the slope are compared between genotypes. The pro of this method is that it discriminates genotypes according to their level of GEI. Its main con is that environments are artificially ranked based on their *a posteriori* performance. Consequently, it has no predictive values.

4.3.1.3. AMMI

In the AMMI model, a fixed effect of G and E analysis of variance is performed at first with no GEI effect. Then, a principal component analysis is done on the non-additive effect (GEI). That methodology has the advantage of helping breeders to select genotypes with low GEI (Debaeke and Quilot-Turion, 2014), however it does not describe the cause of these GEI. This analysis is also made *a posteriori* and depends on the locations tested. It has no use in different environments.

4.3.1.4. GGE biplots

As the AMMI described in section 4.3.1.3, GGE biplots combines both environments and genotypes on the same plot. This method is convenient when it comes to find which couples of E and G are the best match, but has the same drawbacks as AMMI.

All these methods do not provide biological signification of GEI, do not detail the timing of E effect, and have no predictive value. On the contrary, another kind of GEI methods represents mechanisms of biological systems, and has predictive value. These methods are commonly called the crop simulation models (CSM).

4.3.2. Crop simulation models

4.3.2.1. Global description and cultivars traits concept

Most CSM are capable of simulating crop phenology, total above-ground and root biomass, leaf area, yield, and field water balance components in daily time steps. However, they clearly differ with respect to their complexity and algorithms applied (Palosuo et al., 2011). Crop simulation models are developed to either represent potential or limited production. Van Ittersum et al (2003) described the factors that define potential, water or nutrient limited and actual production (Figure 11).

Most of CSM have the ability to differentiate between species, ecotypes and cultivars based on genetic parameters which are the same within the same species, ecotype and cultivar, respectively. Genetic parameters refer to phenology, growth, photosynthesis, water use, and biomass allocation. The importance of these genetic parameters is that it allows model inversion techniques useful for ideotype identification as best combination of crop traits of varieties can be estimate in large field trials, where crop sensors are deployed for field-based high-throughput phenotyping (White et al., 2012).

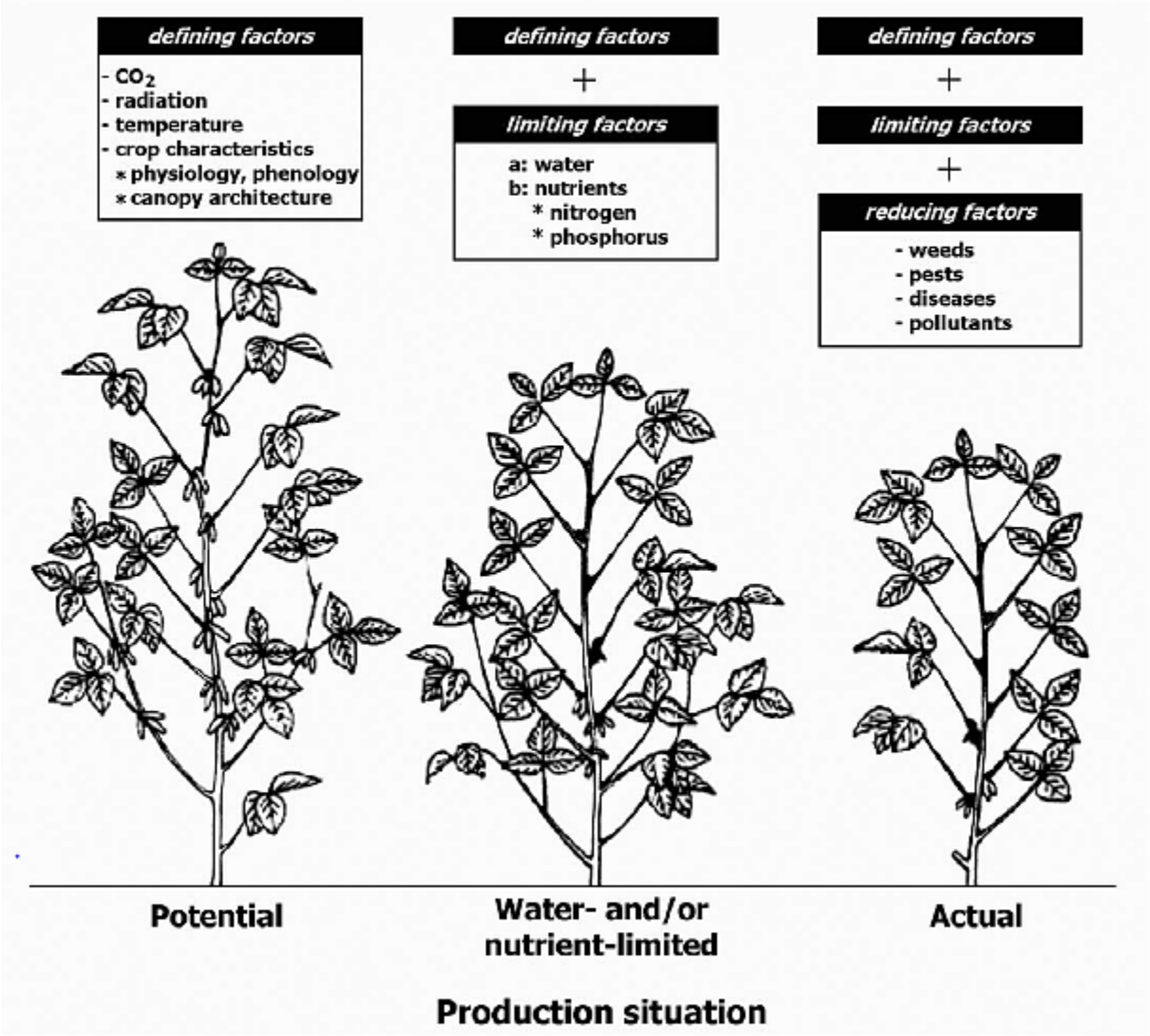

Figure 11. A hierarchy of growth factors, production situations and associated production levels (van Ittersum et al., 2003).

4.3.2.2. Development stages and representation of indeterminate growth

In CSM, the development of the crop usually depends on a sum of photo-thermal days' threshold. Once, the crop reaches this threshold, it joins the next development stage. For each development stage, a set of parameters defines crop sensitivity to environmental conditions, speed of growth, resource allocation etc. Indeterminate crops are commonly represented via allocation function that depends on the vegetative stage. For example, in the very early stages of development, biomass allocation goes to roots and aerial vegetative parts but not to reproductive parts. On the contrary, after the anthesis, most of the biomass is allocated to reproductive organs.

4.3.2.3. Leaf area development and radiation use

Most of CSM simulate a leaf area dynamics that depend on crop phenological stage. Some CSM base their leaf area computation on specific leaf area (SLA) and biomass partitioning and/or a maximum leaf area index. In most CSM, the light utilization and transformation into biomass is described by leaf photosynthesis, respiration, and is development-stage-dependent for dry matter allocation patterns (van Ittersum et al., 2003). Other CSM just use the RUE approach described by Monteith and Moss (1977).

4.3.2.4. Water use

Most models use either a simpler capacity or tipping bucket approach (van Ittersum et al., 2003). Models also require different numbers and types of weather variables, mostly depending on the evapotranspiration formulae applied (Penman–Monteith, Priestley–Taylor). Wu et al (2008) reviewed that model assumptions regarding root distribution over depth and related water uptake vary.

4.3.2.5. Crop simulation model suitable for cotton

Cotton crop was one of the first crops to be modelled. About 15 models have been developed specifically for cotton (see Gérardeaux, 2009). A review paper listed all processes and potential use of main cotton CSM (Thorp et al., 2014). These CSM are GOSSYM (Baker et al., 1983), Cotton2K (Marani, 2004), COTCO2 (Wall et al., 1994), OZCOT (Hearn, 1994; Hearn and Da Roza, 1985), and the Decision Support System for Agrotechnology Transfer (DSSAT) CROPGRO-Cotton (Hoogenboom et al., 1992; Jones et al., 2003). GOSSYM, OZCOT and DSSAT CROPGRO-Cotton have a daily time step whereas Cotton2K and COTCO2 have hourly time step. Table 2 (source: Thorp et al. 2014) shows the processes generating development, growth and yield component of each model. The Table 3 (source: Thorp et al. 2014) shows the environmental factors that are represented in relation to the crop in the 5 cotton CSM.

According to all processes and relations to environmental conditions described before, range of use differs from a CSM to another. Table 4 (source: Thorp et al. 2014) shows that the effect of planting date, cultivar choice, row spacing, plant density and irrigation could be represented by all models. Other management characteristics impact some model but not all. The impact of skip row practices is not available in COTCO2 and DSSAT CROPGRO-Cotton. Fertilizer impact on the crop cannot be studied with COTCO2. The only CSM considering tillage impact on the system are Cotton2K and DSSAT CROPGRO-Cotton. In addition, effect of crop residue on the system can only be studied by DSSAT CROPGRO-Cotton. Growth regulators impact can only be studied with GOSSYM and Cotton2K. Defoliation is represented in all models except COTCO2. Considering

environmental studies, the impact of insect damage is represented in all models. Disease impact is only represented in Cotton2K and DSSAT CROPGRO-Cotton. The climate change (due to CO2) can only be studied with GOSSYM, COTCO2, and DSSAT CROPGRO-Cotton. Cropping sequences (long term studies) can only studied by OZCOT and DSSAT CROPGRO-Cotton. Finally geospatial analyses are only available in Cotton3K, OZCOT and DSSAT CROPGRO-Cotton.

Table 2. Crop growth and development processes simulated by existing cotton simulation models.
(Thorp et al. 2014)

	GOSSYM	Cotton2K	COTCO2	OZCOT	DSSAT CROPGRO-Cotton
Phenology	Develops vegetative and fruiting branches and nodes based on thermal time. Calculates the number of branches, squares, bolls, open bolls, fruiting sites, and aborted fruits.	Develops vegetative and fruiting branches and nodes based on thermal time. Calculates the number of branches, squares, bolls, open bolls, fruiting sites, and aborted fruits.	Develops meristem tissue, leaf primordia, petioles, growing and mature leaves, stem segments between nodes, squares, bolls, and open bolls based on thermal time.	Develops the number of fruiting sites based on thermal time. Calculates the number of squares, bolls, open bolls, and aborted fruits based on crop carrying capacity.	Develops proceeds through growth stages based on photothermal time: emergence, first leaf, first flower, first seed, first cracked boll, and 90% open boll. Calculates boll number and aborted fruits.
Plant maps	Yes	Yes	Yes	No	No
Potential carbon assimilation	Canopy-level radiation interception	Canopy-level radiation interception	Organ-level biochemistry (Farquhar et al., 1980)	Canopy-level radiation interception	Leaf-level biochemistry (Farquhar et al., 1980)
Respiration	Uses an empirical function of respiration based on biomass and air temperature	Calculates growth and maintenance respiration and photorespiration	Calculates organ-level growth and maintenance respiration and photorespiration	Uses empirical functions of respiration based on fruiting site count and air temperature	Calculates growth and maintenance respiration
Partitioning	Allocates carbon to individual growing organs	Allocates carbon to individual growing organs	Allocates carbon to individual growing organs	Allocates carbon to cohort pools for developing bolls	Allocates carbon to single pools for leaves, stems, roots, and bolls
Canopy size	Calculates plant height	Calculates plant height	Calculates stem segment lengths	None	Calculates hedgerow-based canopy height and width
Yield components	Calculates fiber mass as a fraction of boll mass and boll size	Calculates burr mass and seed cotton mass	Calculates boll mass	Calculates fiber mass as a fraction of boll mass and boll size	Calculates boll mass, seed cotton mass, seed number, and unit seed weight
Stress	Calculates stress due to water, nitrogen, and air temperature	Calculates stress due to water, nitrogen, and air temperature	Calculates stress due to water and air temperature	Calculates stress due to water, nitrogen, and air temperature	Calculates stress due to water, nitrogen, and air temperature

Table 3. Atmospheric and soil processes simulated by existing cotton simulation models
(Thorp et al. 2014)

	GOSSYM	Cotton2K	COTCO2	OZCOT	DSSAT CROPGRO-Cotton
[CO2] effect on photosynthesis	Yes	Yes	Yes	No	Yes
[CO2] effect on transpiration	No	No	Yes	No	Yes
Evapotranspiration	Ritchie (1972)	Modified Penman equation from CA Irrigation Management Information System	Leaf-level energy balance coupled with stomatal conductance	Ritchie (1972)	Priestley and Taylor (1972) and FAO-56 (Allen et al., 1998)
Soil water	2D RHIZOS model (Lambert et al., 1976)	2D RHIZOS model (Lambert et al., 1976)	2D model	Ritchie (1972)	Ritchie (1998) and Ritchie et al. (2009)
Soil nitrogen	Dynamic simulation of soil and plant nitrogen balances	Dynamic simulation of soil and plant nitrogen balances	No	Static, empirical apporach that predicts potential N uptake	Godwin and Singh (1998) or Gijsman et al. (2002)
Soil phosphorus	No	No	No	No	Yes
Soil salinity	No	Yes	No	No	No
Waterlogging	No	No	No	Yes	Yes
Flooding	No	No	No	No	Yes

Table 4. Management practices simulated by existing cotton simulation models and possible applications.
(Thorp et al. 2014)

	GOSSYM	Cotton2K	COTCO2	OZCOT	DSSAT CROPGRO-Cotton
Sowing date	✓	✓	✓	✓	✓
Cultivar selection	✓	✓	✓	✓	✓
Row spacing	✓	✓	✓	✓	✓
Skip rows	✓	✓		✓	
Planting density	✓	✓	✓	✓	✓
Irrigation	✓	✓	✓	✓	✓
Fertilizer	✓	✓		✓	✓
Crop residue					✓
Tillage		✓			✓
Growth regulators	✓	✓			
Defoliation	✓	✓		✓	✓
Insect damage	✓	✓	✓	✓	✓
Disease impact		✓			✓
Climate change	✓		✓		✓
Cropping sequences				✓	✓
Geospatial analysis		✓		✓	✓

5. Problem statement of the thesis

In northern Cameroon, seed cotton yield per hectare showed a large inter-annual variability and has levelled off for more than thirty years now (Figure 12) or is even decreasing steadily since the 80s (Naudin et al. 2010). In Sub Saharan Africa, length of the season available for crop growth tends to decline (Vrieling et al., 2013) and climatic scenarios predict higher variability of rainfall (Sultan et al., 2010). In addition, lint yield has important GEI in Cameroon (Figure 13). Indeed, cultivar V2088 showed lower lint yield in the North region and higher lint yield in Far North region compared to control.

5.1. Hypothesis

Since cotton breeding is performed under rainfed conditions, it should have selected cultivars with traits adapted to the local conditions, characterized by early water stresses (July/August) and short rainfall duration (<90 days). Analyzing GEI of growth and development of the main cotton cultivars grown from 1950 to 2009 will let us estimate the genetic gain, especially the one related to adaptation traits to drought conditions indirectly selected. Analysis, modelling and simulation of GEI should help predicting yields, and optimizing management (ideotypes, crop practices) in future conditions facing climate change.

5.2. Goal and objectives

The goal of this thesis is to develop a complementary methodology for breeding cultivars in rainfed conditions. The demonstration is based within the cotton development company in Cameroon (Sodecoton) whose main objectives are to: increase lint (and seed cotton) yield per hectare, crop sustainability, and fiber quality.

The main objective of this study is to model GEI in order to define ideotypes for rainfed cotton in Cameroon.

The specific objectives are to:

(i) Evaluate phenotype evolution over breeding time of some widely grown cotton cultivars released in Cameroon from 1950 to 2009.
   - Do recent cultivars have adaptation traits to the cotton production area in Cameroon?

(ii) Analyze GEI under water limited conditions for a subset of cultivars.

(iii) Calibrate, validate and use a CSM in Cameroonian cotton cropping conditions for the design of ideotypes.
   - Does the CSM represent GEI under water limited conditions?
   - Which are the characteristics of rainfed cotton ideotypes in Cameroon?

An application of this work could be in developing key measurements targeting drought adaptation traits for cotton. Breeders should include in their breeding program such measurements in order to target the best cultivars for rainfed conditions in northern Cameroon.

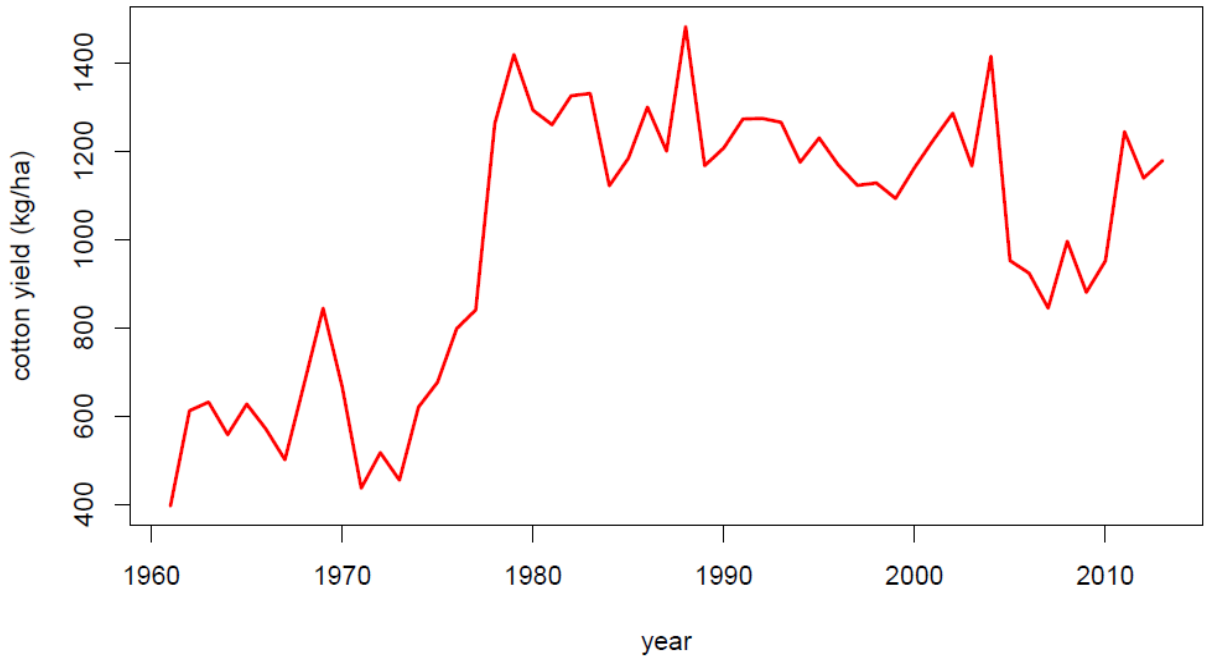

Figure 12. Seedcotton yield (kg ha^{-1}) in Cameroon from 1961 to 2013.
(Source : Sodécoton,2013)

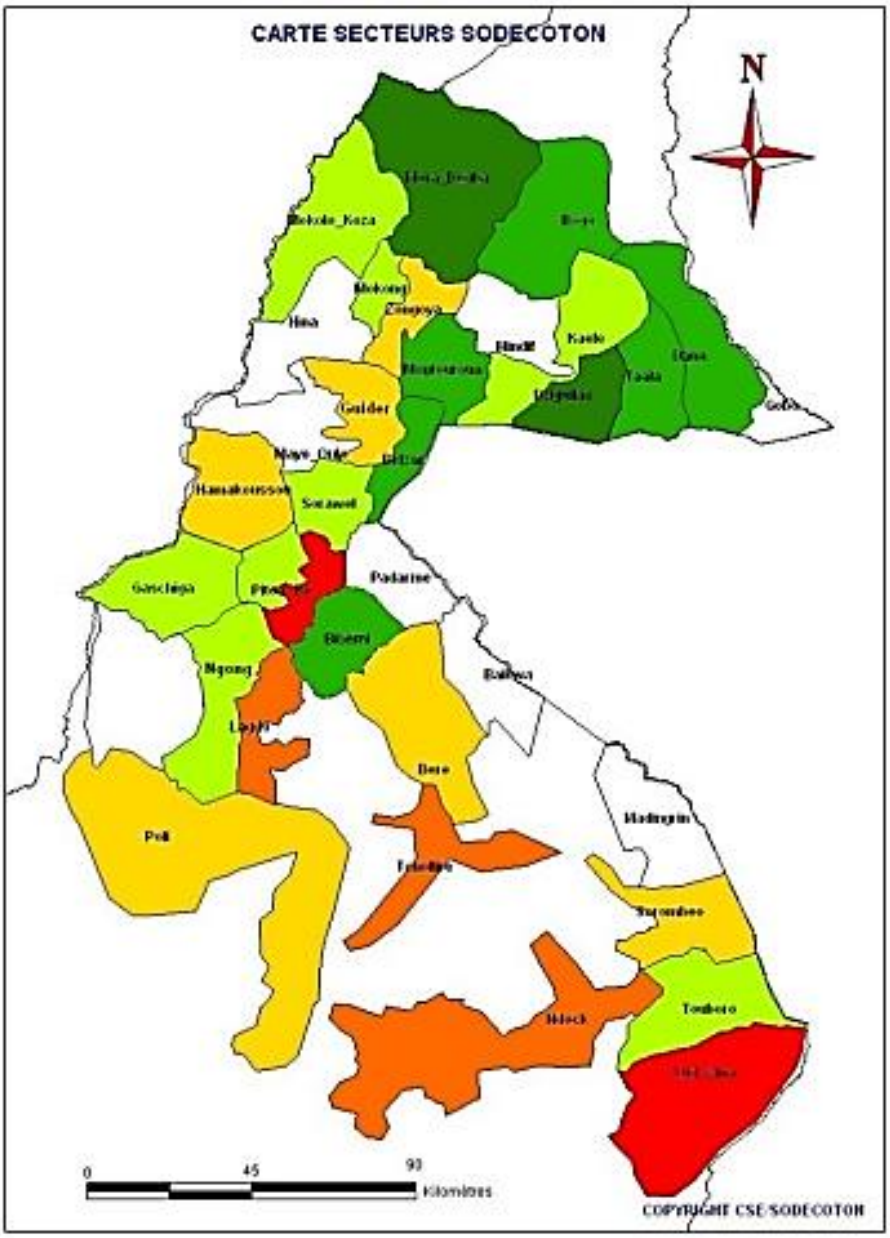

Figure 13. Comparison of two cultivars lint yield in the cropping seasons 2012 to 2014 in Cameroon.

Presence of Genotype x environment interactions. In yellow, orange, and red, V2088 yielded better than L457. For greens, it was the contrary (Genetic Annual Report 2013-14, Sodécoton).

5.3. Methodology

5.3.1. Dissection of historical cultivars

In this chapter, evaluation of interaction between cotton genetic gain and cropping conditions in Cameroon is done on development, growth, radiation use, and yield and fiber quality. This chapter also includes the analysis of genetic gain on the root properties of cotton.

Ten major cultivars were used in field rainfed conditions, in non-limiting greenhouse conditions, and in a phytotron (root studies).

We used classical GEI analysis of variance (section 4.3.1.1) as cultivars were represented as a quantitative independent variable using their year of release. There were only 3 environments compared with contrasted analysis.

5.3.2. From 10 to 4 cultivars: Principal Component Analysis

The objective here was to reduce the number of cultivars in order to be able to increase the number of morpho-physiological traits to consider and the microplot area and replication number in the field. A principal component analysis was performed based on section 5.3.1 observations.

5.3.3. Mechanisms

Here, the ecophysiological traits that could confer a good response to drought among genotypes grown in Cameroon in the past or nowadays are evaluated. In order to compare radiation use efficiency (Monteith and Moss, 1977), water use efficiency (Passioura, 1996) and efficient use of water (Blum, 2009) in drought conditions; a subset of 4 cotton genotypes were compared in field trials under potential and water-limited conditions but also in greenhouse experiment where water conditions are more easily controlled. Soil water balances were performed (PROBE-W, model developed by Chopart and Vauclin (1990) for tropical regions) in order to discriminate cropping conditions. Four cultivars were cultivated in field rainfed conditions and in water-limited vs non-limiting greenhouse conditions. In this section, physiological traits and elementary variables are used. This along with the reduced number of cultivars made classical GEI analysis of variance (section 4.3.1.1) easy to perform and sufficient. Variables of interest were selected based on a generic conceptual framework of crop growth and development that we attempted (Figure 14). This framework applied to cotton relates yield to biomass production, and biomass to radiation and water use components.

The radiation use description focuses on light interception and transformation into biomass through photosynthesis. The main effective interception organ is the leaf compartment. It is dynamically described by the leaf number, dry mass, specific leaf weight (SLW). In addition, the average single leaf area depends on the leaf expansion rate. The total leaf area at a particular date

is the product of the leaf number and the average single leaf area at that date. The chlorophyll in the total leaf area intercepts light every day and transforms it into biomass through photosynthesis. An indicator of the photosynthetic capacity is the radiation use efficiency (RUE), calculated as the ratio of total dry aerial biomass to the amount of photoactive radiation intercepted.

The water use description focuses on water uptake and transformation into biomass through photosynthesis. The plant's water uptake organ is the root compartment. It is described by the dynamic change in root depth and soil occupancy. The uptake of water by the root compartment is mainly transpired by the leaf compartment. Leaf area dynamic is important because when it increases, soil evaporation decreases and transpiration increases.

Finally, biomass produced is allocated to new organs and is maintained throughout the crop cycle when no particular stress occurs or otherwise shed off. The harvest index is the ratio of cotton yield (seed and lint) to the total aerial biomass.

The radiation use description will be analyzed based on field and greenhouse experiments. The water use description, on greenhouse experiment. Finally, the biomass description, on field experiments.

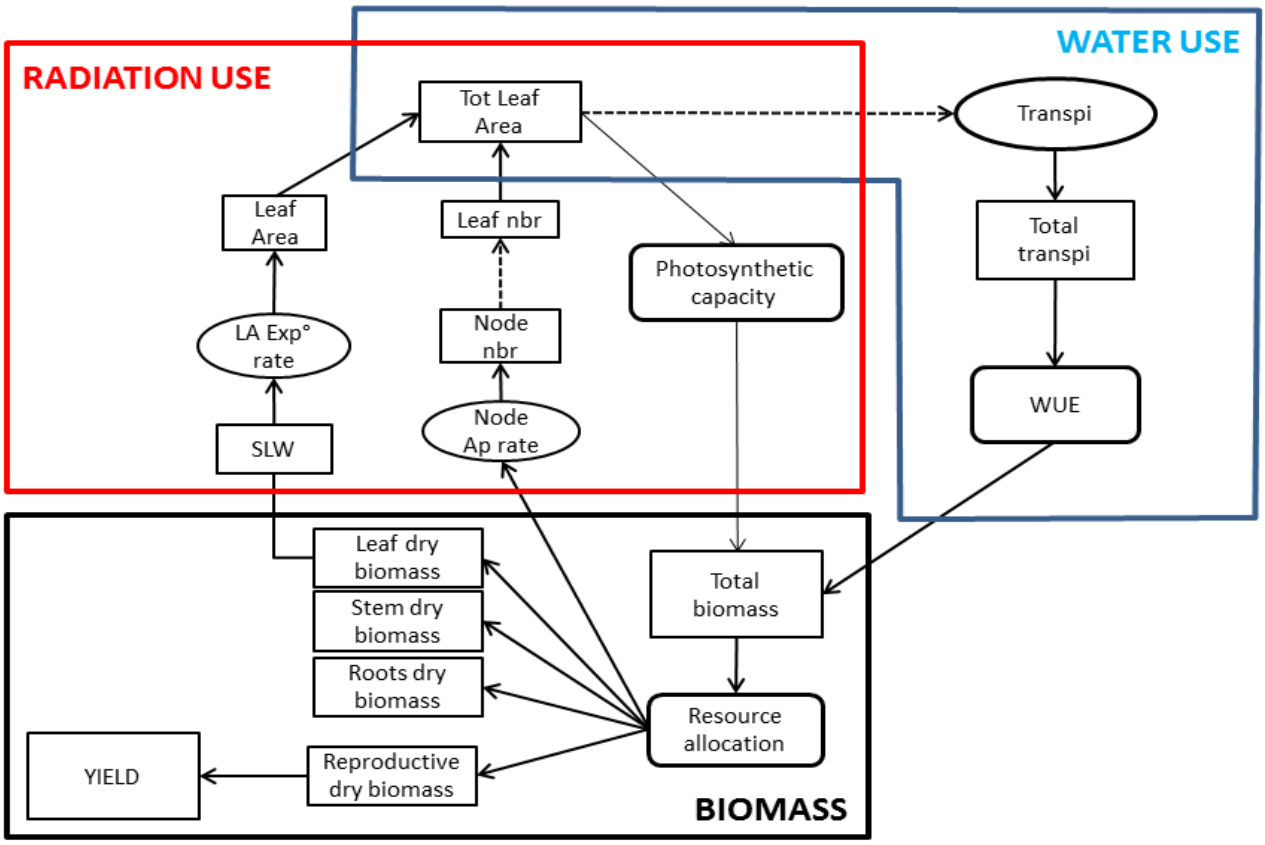

Figure 14. Generic model of radiation use, water use and plant biomass allocation.

5.3.4. Modelling

5.3.4.1. Justification of model choice; why DSSAT?

In our study, we want to simulate the effect of planting dates, level of fertilization, soil management, and rainfall pattern on growth, development, and yield of several cotton cultivars in Cameroon. According to section 4.3.2.5, only the CSM CROPGRO-Cotton provided by DSSAT and the Cotton2K CSM can be used in our study. In Cameroon, the conservation agriculture should be considered as an alternative to conventional practices in order to overpass cotton yields levelling off (Naudin et al., 2010). Consequently, crop residual and long term effect should also be considered in our study. DSSAT CROPGRO-Cotton is the only CSM considering the impact of soil residues on the system (section 4.3.2.5). In addition, in DSSAT a soil subroutine (CENTURY) could represent long term evolution of soil fertility for C and N (Smith et al., 1997), and therefore the long term effect of practice can be simulated. We concluded that the best CSM for our study is DSSAT CROPGRO-Cotton. Additionally, its minimum dataset is small enough to be implemented without too extensive measurement and at a moderate cost. Few additional measurements during breeding process in Cameroon should be sufficient for calibration. In addition, the DSSAT CSMs have already been extensively used in Africa (Jones and Thornton, 2013; L. D. Estes et al., 2013; Dube et al., 2013; Lyndon D. Estes et al., 2013; Ya-nan et al., 2014; Kassie et al., 2014; Rezaei et al., 2014; Ngwira et al., 2014; Zinyengere et al., 2014; Yang et al., 2014), for cotton (Cabrera et al., 2006; Suleiman et al., 2007; Garcia y Garcia et al., 2008; Yang et al., 2010; Garcia y Garcia et al., 2010; Soler et al., 2011; Dzotsi et al., 2013; Thorp and Bronson, 2013; Wajid et al., 2014; Ortiz et al., 2009), and for cotton in Africa (Gérardeaux et al., 2013). Another important advantage is that DSSAT is free and there is an extensive population of scientists still working with and on it as mentioned by bibliography (182 references in Web of Science from 1st January 2010 to evaluation made on January 18, 2015).

Based on all these arguments, we selected CROPGRO-Cotton as our candidate for the representation of GEI in cotton crop in Cameroon.

5.3.4.2. Calibrating and validating

Field experiments in Cameroon were used to constitute the minimum dataset for calibration: weather, soil characterization, cropping management, yield, leaf area index and main phenologic stages were required. A range of conditions (from best to highly limiting) were used for the model calibration (G0 2012, G0 2013, G1 2013, and M1 2012; Table 5). Other cropping conditions were used for validation (G1 2012, G2 2012, M0 2012, S0 2013, and S1 2013) including data coming from another location (Soukoundou). A tool in DSSAT, GenCalc, was used several times to calibrate

and obtain the genetic parameters. Some other parameters were also changed manually when accurate measurements were possible. Calibration and evaluation of the 2 most different cultivars according to section 5.3.3 was performed (AC and L484).

5.3.4.3. Exploration: Design of ideotype

Once calibrated and validated for cultivars AC and L484, CROPGRO-Cotton was used to evaluate these two cultivars in a range of 99 climatic years generated by WGEN (Richardson, 1985, 1981) from a dataset from the NASA. Based on the results of the simulation, we tried to identify ideotypes.

5.3.5. Summarizing: Description of all experiments done

Table 5 synthetically represents the correspondence between experiments and their purpose.

Table 5. Objectives of the study and corresponding experiments.

Experiments	Historic	Mechanisms	Model calibration	Model validation
Greenhouse potential	✓		✓	
Phytotron	✓			
Greenhouse water limited		✓	✓	
Fields in Cameroon				
2012				
Sanguéré (North region)				
G0: early planting	✓	✓	✓	
G1: mid-late planting	✓	✓		✓
G2: late planting	✓	✓		✓
Kodeck (Far North region)				
M0: early planting	✓	✓		✓
M1: late planting	✓	✓	✓	
2013				
Sanguéré (North region)				
G0: early planting		✓	✓	
G1: late planting		✓	✓	
Soukoundou (North region)				
S0: early planting		✓		✓
S1: late planting		✓		✓

Genetic improvement of cotton in Cameroon

This chapter was adapted from Loison, R., Audebert, A., Chopart, J.C., Debaeke, P., Dessauw, D., Gourlot, J.P., Gozé, E., Jean, J., and Gérardeaux E. Sixty Years of Cotton Breeding in Cameroon: Interaction between Genetic Improvement and Rainfed Cropping Conditions. In preparation.

Abstract

Seed cotton (*Gossypium hirsutum* L) yield in Northern Cameroon has been declining since the 80s despite breeding efforts. We used a set of widely grown cotton cultivars released at different dates to study genetic improvement under different cropping conditions in Cameroon, and in controlled conditions. The genetic gain was estimated with a linear regression of the variety mean on its year of release (YR). Contrasts between genetic gains observed with different planting dates were estimated and tested. Our results revealed a genetic improvement on fiber yield of 3.3 kg ha^{-1} $year^{-1}$ due to increased ginning out-turn. However, there was no genetic improvement on aerial biomass, harvest index or seed cotton yield. At the early stage of development, aerial and root biomass, and potential root extraction ratio of nutrients decreased with YR. So did leaf number and hairiness at the beginning of flowering. Carbon dioxide assimilation was not affected by YR. Neither were crop cycle duration and phyllochron. Although the potential of almost all fiber technological characteristics was improved under favorable water conditions, some (upper half mean length, short fiber index, uniformity index, and strength) were reduced in water-limited conditions. We concluded that cotton breeding efforts in Cameroon have successfully improved cotton fiber yield and the potential of most fiber technological characteristics. However, in water-limited conditions, fiber quality tended to decrease with the YR. There is still some room for seed cotton yield improvement.

1. Introduction

Cotton is a source of income for more than 10 million people in West and Central Africa (Baffes, 2004). In Cameroon, during the last decade, cotton farming provided a global yearly income of between US$ 33 to 111 million shared by 240 000 growers (*Source: Sodecoton 2014*). The cotton sector (agronomy, ginning and oil industries) is a major economic driver in the North and Far North regions where cotton is produced in rainfed conditions (Sultan et al., 2010). Water availability during the crop cycle, characterized by the length and the quality of the rainy season has a tremendous importance on cotton production (M'Biandoun and Olina, 2006). In addition, other agronomic and socio-economic factors such as soil fertility, pests and competition with food crops, have made cotton a challenging crop to grow in Cameroon.

Each stakeholder in the cotton industry of Cameroon has specific objectives and constraints. Cotton farmers sell their production (seed cotton) to the development company (Sodecoton) and aim at producing a lot of cotton per unit land area. Sodecoton buys the seed cotton from farmers and after ginning, sells the fiber to the international market and the local spinning industry. Sodecoton aims at getting a large amount of cotton fiber of high quality to sell to the international market and to meet the specifications of the spinning industry. Finally, the spinning industry looks for a compromise between fiber quality, price and how fast it can be processed as a function of the desired product.

In this context, a breeding program was initiated in Cameroon in 1950 with the objectives of increasing the fiber yield, the resistance to pests and diseases, and improving the fiber technological characteristics (Levrat, 2010). The breeders were closely working with Sodecoton, and were following its specifications. Breeders developed new cultivars genealogically (pedigree method with self-pollination) using crosses between parental lines both from Africa (Mali, Cameroon and Ivory Coast) and the USA or other origins. Then from the generation F2 until F4, individual plants were selected, and the self-pollinated seeds of one plant were planted in one line for the next generation. This procedure was repeated for four consecutive years to achieve line stabilization. In the F5 generation, families were selected and thereafter local and multi-local agronomic assessment of the best stabilized lines was performed under rainfed conditions. Plants selected by breeders in the field should not be diseased, should have a minimum number of developed vegetative branches, many large bolls with wide and early opening, moderately hairy leaves, and short internode length. The plants with these characteristics were evaluated in the laboratory. Plants with high ginning out-turn (greater than 42 %), and high seed unit mass (greater than 9 g) are selected for extra analysis. Fibers of these plants were analyzed. The main criteria

evaluated are micronaire, length, strength, maturity, length uniformity, yellow index and reflectance. For lines selected in generation F5, crop earliness and yield on two locations in contrasted ecological zones were also evaluated. Extensive root systems are vital when plants are grown in soils containing insufficient supplies of water or nutrients (Bengough et al., 2011), but comes at carbon costs not consistent with optimizing yield (Eissenstat, 1997). Unfortunately, breeders cannot measure root properties in the field, as it would be too tedious and costly considering the important number of lines to evaluate. After sixty years of cotton breeding in Cameroon more than twenty cultivars were released.

Despite the breeding program, Naudin et al. (2010) showed that cotton yield has been decreasing steadily since the 80s in northern Cameroon. Cao et al. (2011) showed that increasing numbers of farmers are adopting cropping practices that are unsuitable for cotton, such as reducing fertilizer application, cultivating infertile plots, and planting late in the season. In Cameroon, delayed planting date has a tremendous impact as it can lead to an insufficient length of rainy season available to the cotton crop (M'Biandoun and Olina, 2006). In this context, cotton genetic gain should be evaluated to understand if recently bred cultivars respond better to water limited conditions compared to the old ones.

Many studies have evaluated genetic improvement of yield components, yield and morpho-physiological traits on soybean (Christenson et al., 2014; Koester et al., 2014), peanuts (Wells et al., 1991), wheat (Battenfield et al., 2013), sweet corn (Bunce, 2011), tomatoes (Barrios-Masias and Jackson, 2014), tobacco (Sarcevic et al., 2013), cowpea (Kamara et al., 2011), broccoli (Farnham et al., 2011), cotton (Schwartz and Smith, 2008a) and cotton fiber (Campbell et al., 2011; Schwartz and Smith, 2008b). Most of them used widely grown cultivars in similar environments and they estimated linear or break-linear regressions of dependent variables with the year of release of cultivar (YR). In some other studies, the interactions between genetic improvement and several aspects of the environment were studied. For exemple, the plant density on corn yield (Ci et al., 2011), soybean yield (Suhre et al., 2014), and cotton yield and quality (Schwartz and Smith (2008a) and Schwartz and Smith (2008b), respectively). Similarly, the level of fertilization on cotton yield (Meredith et al., 1997); the planting dates on soybean yield and phenology (Rowntree et al., 2014); potential of the environment on cotton yield and fiber quality (Campbell et al., 2012) were also studied.

Campbell et al. (2012) and Liu et al. (2013) showed significant interactions between genetic improvement on cotton yield and environment in the USA and Australia, respectively. In Cameroon where cotton is grown in a wide range of environmental and crop management conditions,

resulting from various onsets of rains, sowing dates, fertilization rates, weed control methods, and insect attacks, genetic improvement should be assessed on a diverse set of production situations.

We mentioned previous studies on cotton yield and fiber quality genetic improvement. However, it has never been evaluated on cotton in Africa, and the consequences on rooting system has never been evaluated either so far. Likewise, the interaction between cotton genetic improvement and planting date in Africa has never been studied. Finally, no study has evaluated the genetic improvement on Cameroonian cotton development, growth, radiation use, cotton yield, and fiber quality.

Therefore, the objectives of this paper are:

i/ estimating over several Cameroonian environments the genetic improvement in development and growth, radiation use components, yield components and fiber quality on a set of cotton cultivars released between 1950 and 2009;

ii/ determining whether genetic improvement is affected or not by the main source of environmental variation of cotton crop in Africa: the planting date.

To this end, i/ a set of widely grown cultivars from different origins and with different YR were compared in field trials in Cameroon, and controlled conditions (greenhouse, phytotron) at the 'Centre de Coopération Internationale en Recherche Agronomique pour le Développement' (CIRAD), in Montpellier, France. For each variable, in each location, the genetic gain was estimated with a linear regression of the variety mean on its YR, since there was no major shift in breeding targets over these 60 years in Cameroon. ii/ in one location, the contrast between genetic gains observed with different planting dates was estimated and tested.

2. Material & methods

2.1. Plant material

We selected ten cotton cultivars widely cultivated (> 100 000 ha, Table 6) and released in Cameroon at different years spread across and representative of the period 1950 to 2009. Seeds used for this study were coming from one of the world's major cotton germplasm at CIRAD in Montpellier, France (Campbell et al., 2010). Most cultivars grown in Cameroon derived from Allen Commun and N'Kourala as bulk parental lines with other foreign cultivars. For more detailed information on genetic relationship between cultivars and origins, see Figure 7.

Table 6. Cumulated cultivated area (in 10^3 ha) per decade and year of release of main cotton cultivars grown in Cameroon.

Period of cultivation	Allen Commun + N'Kourala	Allen 333-57	IRCO 5028	IRMA 96+97	IRMA 1243	IRMA A1239	IRMA D742	IRMA L484	IRMA L457
1950-1960	108								
1960-1970		529							
1970-1980			38						
1980-1990			238	213	175				
1990-2000				62	1,151	7			
2000-2010					128	945	192	105	27
> 2010						20		>200	>200
∑area (10^3 ha)†	108	529	276	275	1,454	972	192	> 305	> 227
Year of release	1950	1959	1974	1981	1985	1996	1999	2008	2009

† Cumulated area in 1000 hectares.

2.2. Experimental conditions

2.2.1. Field conditions

In 2012, one field experiment was arranged as a randomized block design, with one factor and three replicates in Maroua (10° 39' N, 14° 25' E, and altitude: 380 m), a region of production with limited rainfall. The factor under study was the cotton cultivar with ten levels as described in section 4.1. Another field experiment was set the same year as a split plot design with two factors and three replicates in Garoua (9° 15' N, 13° 28' E, and altitude: 250 m) in wetter conditions. Each unit plot size was 32 m^2 with 5 rows of 8 m. Texture of soil was loamy sand in Garoua and loam in Maroua. Soil depths were 2.0 m and 1.4 m in Garoua and Maroua. Previous crop was a fallow in Garoua and soybean in Maroua.

Soil was ploughed with tractor disks on 13 and 12 June in Garoua and Maroua, respectively. Plant density was 31250 plants ha^{-1} with a row width of 0.8 m in the two locations.

The whole plot factor was the planting date with three levels as described below, and the subplot factor was the cotton cultivar with the same levels as in Maroua. In Garoua, G0 was planted on 14 June, G1 on 27 June, and G2 on 11 July 2012. In Maroua (M0), planting date was 6 July 2012.

Levels of fertilization depended on planting dates and followed the recommendation of Sodecoton. General fertilizer (NPKSB 22-10-15-5-1%) was first applied just after thinning at 200, 150, 100 and 200 kg ha^{-1} in G0, G1, G2, and M0, respectively. A supplemental amount of 23 kg ha^{-1} of urea was applied at ridging in early planting (G0) and mid planting (G1) conditions in Garoua. Pests were controlled with recommended insecticides under rainfed conditions.

Climatic data, including solar radiation, were recorded hourly with synoptic weather stations (iMETOS, PESSL instruments GmbH, Weiz, Austria) installed on each experimental site less than 10 km from the field. Rainfall was recorded daily at less than 100 m from the field.

In Garoua, the rainy season available for cotton started in June and ended in October, whereas in Maroua, it started in July and ended in September. Each month total solar radiation was about 500 MJ m^{-2} during the rainy season, and more than 600 MJ m^{-2} after the end of the rainy season in Garoua. In Maroua, solar radiation was low in August due to heavy cloud cover and rains. Total amount of rainfall from planting to harvest was 1116, 1063, 921, and 671 mm in G0, G1, G2, and Maroua, respectively. Duration of rainy season experienced by the crop (from planting to the last rain above 10mm before harvest) was of 121, 108, 94, and 84 days in G0, G1, G2, and Maroua, respectively. In two conditions (M0 and G2), crops did not reach physiological maturity before the end of the rainy season (estimated at 94 days after emergence (Gérardeaux et al., 2013)).

2.2.2. Greenhouse conditions

The greenhouse experiment was carried out at CIRAD in Montpellier (France) in 2012. Planting date was February 2. Plants were harvested on June 26. The experiment was arranged as a factorial randomized block design with one factor and four replicates. The studied factor was the cotton cultivar. All plants were well watered all cycle long with daily automatic irrigation.

Each experimental unit was a single cotton plant in a 18.5 liters pot (h 30 cm x Ø 30 cm). The growing medium was commercial potting soil with pH = 6 and water holding capacity of 80 % (Neuhaus N°9, ANGIBAUD & SPECIALITES). Optimal fertilization was applied at planting with slow release fertilizer (Basacote Plus 6M; COMPO) homogeneously mixed with potting soil at 3.5 g l^{-1}.

Greenhouse air temperature was automatically adjusted for optimal cotton growth: 30 °C daytime and 25 °C nighttime. There was a sodium light supply from 7:00 to 9:00 am and 5:00 to 7:00 pm (100 µmol m^{-2} s^{-1}). Temperature was measured at several points of the crop canopy and was averaged over the greenhouse. Photoactive radiation was measured with a quantum sensor (LI190SB-L; Campbell Scientific; Logan, Utah, USA) placed on top of the canopy. Hourly weather data were recorded in a data logger (CR-10X; Campbell Scientific; Logan, Utah, USA).

2.2.3. Phytotron conditions

In 2012, a root description experiment was conducted in the Rhizoscope device (described by Courtois et al., 2013) at CIRAD, Montpellier, France. It was set as a fully randomized design with four replicates. Each experiment unit was a single cotton plant which was grown in a sandwich of two 50x20 cm Plexiglas plates filled with glass beads of 1mm diameter called rhizobox (Figure 15). Each rhizobox was 2 cm thick.

After a 48 h pre-germination at 35 °C, plants were grown under 30 °C during the day and 25 °C during the night in an aerated cooled hydroponic nutrient solution as in Courtois et al. (2013). This solution was circulated continuously through the rhizoboxes and its pH was automatically adjusted to 6.5±0.2 and solution temperature was 26.5± 0.8 °C. Each day, the photoactive radiation remained between 400 and 450 µmol m^{-2} s^{-1} for 12 h of day time, and 0 for the 12 hours of night time. The relative humidity was set at 55 %. Each rhizobox contains a grid of nails (2x2 cm), which holds the root system in place after bead removal when the sandwich is opened.

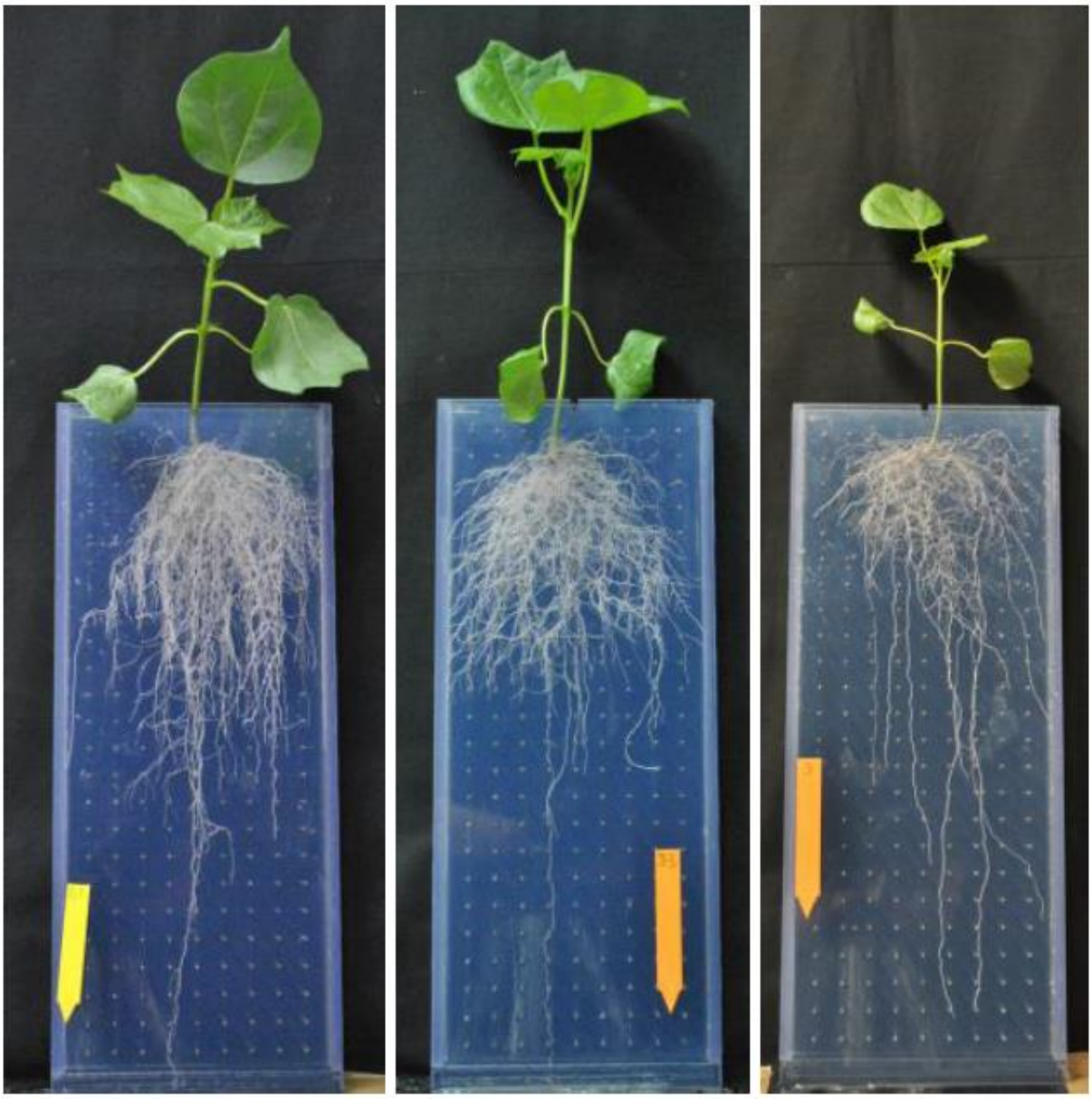

Figure 15. Rhizoboxes showing three cotton plants at 17 days after planting after substrate removal.

From left to right: Cultivar N'Kourala released in 1950, IR9697 released in 1981, and L457 released in 2009. We observed a decrease in biomass (root and shoot) with the year of release. Rhizoscope, Montpellier, France, 2012 (credit: Audebert, 2012).

2.3. Plant measurements

2.3.1. Crop phenology and development

On field, each growth stage was scored as soon as 50 % of the plants in the observed row reached this stage; emergence (both cotyledons fully expanded), anthesis (open flowers) and first open boll. On field and in the greenhouse, the phyllochron was calculated as the ratio of the sum of growing degree days in basis 13 °C (GDD) to the number of nodes appeared during that period of time. In each field plot, 5 consecutive plants were tagged and their number of nodes and height were monitored regularly throughout the growing season until harvest date. At harvest, node number of first fruiting branch and number of vegetative branches were recorded on tagged plants.

2.3.2. Radiation use

On field, leaf area index (LAI) dynamics were recorded with a LICOR LAI-2200 (LI-COR, USA). LAI at 65 days after planting (DAP) was measured in all field cropping conditions. LAI at maximum vegetative stage was measured for G0, G1 and M0 only. Leaf number, average leaf sizes and specific leaf area (SLA) were measured at 65 DAP. SLA was also measured at 65 DAP in the greenhouse.

Leaf hairiness is an indicator of the thickness of leaf boundary layer (Woolley, 1964; Wuenscher, 1970). It was measured at 90 DAP on 5 plants per field plot. A score from 0 (no hair) to 5 (maximum hairiness) was given to each leaf.

In the greenhouse, photosynthesis was measured on the 3rd youngest leaf fully expanded on the main stem at the beginning of anthesis using a portable gas-exchange analyzer (Model GFS-3000, Heinz Walz GmbH). Measurements were done between 9:00 am and 11:00 am. The leaf surrounding volume was set at photosynthetic photon flux density of 1500 µmol m^{-2} s^{-1} and temperature of 30 °C, relative humidity 65 % and [CO2] of 350 ppm. Carbon assimilation rate was defined as in Stuerz et al. (2014).

2.3.3. Crop biomass, yield and yield components

At field level, three plants were randomly chosen for destructive samplings at 65 and 120 DAP. Then aerial dry biomass was determined for each plant compartment (leaves, stems, reproductive organs). Aerial dry biomass per m^2 was assessed from dry biomass per plant and from actual plant density.

Cotton yield was measured on two central rows on an area of 12.8 m^2 per experimental plot. Fiber yield was determined by multiplying cotton yield by the ginning out-turn percentage measured in standard conditions. Harvest index was determined as cotton yield divided by total aerial dry biomass at 120 DAP.

2.3.4. Fiber quality

Ginning out-turn percentage and all fiber technological characteristics were measured using devices of the Natural Fiber Technology and Characterization Laboratory (LTC, Montpellier, France) under its ISO 17025 accreditation system (COFRAC n°1-2386). The ginning out-turn is the percentage of fiber in the seed cotton. It was measured on a eight inches laboratory roller gin (Porter Morrison & Sons 20, Dennis Mfg. Co., Inc., USA) at 21 °C and 65 % of relative humidity. Following fiber technological characteristics were measured with high volume instrument (HVI 1000 M700, USTER). The fiber upper half mean length (UHML, in mm) is the average length of the longer one-half of the fibers. The short fiber index is the percentage of fiber shorter than 0.5 inch. The uniformity index is the ratio between the mean length and the UHML of the fibers and is expressed as a percentage. The fiber strength is determined as the force necessary to break the beard of fibers (in g tex^{-1}). The fiber elongation is the percentage of elongation that the fiber can stand before it breaks. The brightness and yellowness indexes indicate the color of the fiber. Following fiber technological characteristics were measured with a fiber and maturity tester (FMT3, SDL-Atlas). The fiber standard fineness corresponds to the mass of one mature fiber per unit length (mtex). The maturity ratio is an indicator of fiber wall thickness. The micronaire index is an indicator of the fineness and maturity of the fiber. This index is evaluated by the permeability to air of a constant mass of fibers in a fixed volume. All fiber quality measurements were done according to ISO 139 (20 °C ±2 and 65 % ±4 of relative humidity).

2.4. Variables derived from on-field or greenhouse measurements

2.4.1. Plant leaf area

Allometric relationships between leaf dimension and area have been extensively used (Fideles Filho et al., 2010; Grimes and Carter, 1969). For each cultivar, the length of leaf vein localized on the left to the central vein of the upper side (LVL, in mm; vein #4 in Figure 1) was measured using a ruler and leaf area was assessed with a scanner (Model LI-3100-C, LI-COR). A strong allometric relationship between one leaf area (LA, in cm^2) and its corresponding LVL was established on about 50 leaves per variety, as follows:

$$LA = \alpha * LVL^{\beta} \qquad \text{(Eq.1)}$$

Fitting parameters α and β were respectively 0.00667 and 2.093 for AC (R^2= 0.97), 0.0147 and 1.972 for IRCO (R^2=0.97), 0.012 and 1.899 for L457 (R^2=0.96) and 0.00337 and 2.210 for L484 (R^2=0.96). Plant leaf number only considers leaves with LVL > 30mm. Plant total leaf area at date d was calculated as the sum of individual leaf areas at that date. The average area of a single leaf was calculated as the ratio of total leaf area to the total number of leaves of the plant.

The SLA was calculated as the ratio of leaf area to leaf dry biomass after oven drying leaves for 48 h at 80 °C.

2.4.2. Total intercepted photosynthetically active radiation and global radiation use efficiency

Total intercepted photosynthetically active radiation (∑PARint) depends on the coefficient of light extinction *(k)*, leaf area index (LAI) and photosynthetically active radiation (PAR) of each day (Eq.2). For common plant density, *k* was considered constant (0.69) (Brodrick et al., 2013) and the maximum value of light interception that can be attained by the crop (εamax) was set at 95%.

$$\sum PARint = \sum \varepsilon amax * [1-\exp(-k * LAI)] * PAR \quad \text{(Eq.2)}$$

The global radiation use efficiency (RUE) was defined as the ratio of accumulated aerial dry matter to intercepted photosynthetically active radiation over the same period (Monteith and Moss, 1977). In this experiment, global RUE was calculated from 35 to 95 DAP.

2.5. Root measurements in phytotron

At 17 DAP, rhizoboxes were emptied and root traits were measured directly (root growth speed, root angle, biomass and shoot/root ratio), and indirectly by analyzing pictures using ImageJ software (Schneider et al., 2012).

The layer of profile from 0 to 10 cm deep was densely occupied by roots and was not discriminated in our analysis. Each value of root length density (RLD), average distance between roots (RD) (Newman, 1966) and potential root extraction ratio (PRER) (Chopart et al., 2012; Nodichao et al., 2011) were first calculated per homogeneous volume of 8x8x2 cm^3 (width, height, thickness, respectively) from depth of 10 to 34 cm and 12x8x2 cm^3 from depth of 34 to 46 cm.

RLD was calculated using the method of lines intersections (Tennant, 1975). Since the grid unit was 2x2 cm, the value of conversion factor (*conv*) of 1.5714 (Tennant, 1975) was used as follows:

RLD ($cm\ cm^{-3}$) = (Number of root intersections x *conv*)/volume studied (Eq. 3)

The RD was calculated as follows:

$$RD = (\sqrt{(4/\pi)})/(\sqrt{RLD}) \quad \text{(Eq. 4)}$$

In the PRER calculation, we used a maximum distance for water migration in the soil to the root (*max d*) of 5 cm (Chopart, 1996; Dusserre et al., 2009; Lang and Gardner, 1970). Maximum distance for nutrients migration in the soil to the roots used was 0.5 cm.

When RD was strictly inferior to two times *max d,* competition between roots was considered and the equation used for the calculation of the PRER in each cell was as follow:

$$PRER = 1 - RD/(3 * max\ d) \quad \text{(Eq.5)}$$

When RD was superior to two times *max d,* no competition for water (or nutrients) was considered and the equation used for the calculation of the PRER in each cell was as follow:

PRER = 4/3 * (*max d*/ RD)^2 if Nb root intersection >0 (Eq.6)

PRER = 0 if Nb root intersection =0

Finally, RLD, RD and PRER were averaged over the cells measured.

2.6. Statistical analyses

In each site, an analysis of variance with the appropriate model for the design was performed, and the cultivar means estimated (adjusted means in case some data were missing). Then a linear regression of the (adjusted) means against the YR was performed. The resulting analysis is equivalent to fitting a linear model with a fixed effect of the YR, and a random departure of the variety mean from the linear trend. On the Garoua data, a linear model with contrast estimation was also used to test the interaction between the YR and the date of planting, which is the difference in slope observed under different planting dates. At Garoua, only the latest planting date resulted in an incomplete physiological maturity (Gérardeaux et al., 2013). Thus, the contrast was the difference in slope between the latest planting date (G2) and the mean of the two earlier ones (G0+G1)/2. When this contrast in slopes was not significant, only the mean rate of genetic gain was considered, and presented in italics in tables 8, 9, 10, 12, and 13. When this contrast in slopes was significant at 5% level, the rate of genetic gain was considered separately for each planting date, G0, G1, and G2, and the three slopes were presented in italics. Maroua M0 was not included in the contrast as many conditions other than planting date differed between Garoua and Maroua (rainfall pattern, temperatures, radiation, soil, etc.).

The analyses were performed with the mixed and glm procedures of SAS [SAS 9.4 software, of the SAS System for Windows. Copyright © 2014 SAS Institute Inc., Cary, NC, USA].

Root data were analyzed using R software (R Core Team, 2014). Simple linear model were used with the YR as the quantitative factor.

Model used for statistical analyses of data from Garoua:
Gain = YR + planting date + planting date x YR + *block* + *block x* planting date + ε
For Maroua or the Greenhouse:
Gain = YR + *block* + ε
For the phytotron:
Gain = YR + ε
YR: year of release of a cultivar
planting date: whole plot factor in Garoua, 3 levels: early, mid and late planting
block: random effect of the block
block x planting date: whole plot error
ε: residual error at sub-plot level

3. Results

The effect of cropping conditions alone on level of each variable was not of interest. Nevertheless, in order to provide the range of cotton performance in this study, one can find the (adjusted) means of all variables by cropping condition, across cultivars in Appendix 1. We focused on evaluating the genetic improvement associated with the YR and its dependence on cropping conditions. The early (G0) and mid-late (G1) plantings in Garoua were considered as favorable based on the length of rainy season available for the crop cycle (121 and 108 days, respectively). Late planting in Garoua (G2) and Maroua (M0) were considered as unfavorable, with 94 days and 84 days of rainy season for the crop cycle, respectively.

For all variables except the number of vegetative branches, no significant difference of genetic gain between early planting (G0) and mid planting (G1) in Garoua was found (results not shown). For these planting dates, the rate of genetic gain was always considered to be the same.

3.1. Yield and its components

There was no difference between cropping conditions in Garoua on all rates of genetic gain on the yield and its components (Table 7). There was also no significant increase in seed cotton yield with the YR, across all cropping conditions in Garoua (Figure 16a) as in Maroua (Table 7). On the contrary, the fiber yield has been significantly increased for early planting (G0) and mid-planting (G1), but not for late planting (G2) in Garoua (Figure 16b). Nonetheless, only the mean rate of genetic gain is considered for fiber yield in Garoua. Fiber yield showed a yearly rate of genetic gain of 3.3 kg ha^{-1} in Garoua. In Maroua, no significant genetic gain was observed on fiber yield. The ginning out-turn has been significantly increased in G0 and G2 but not in G1 (Figure 16c). Nonetheless, only the mean rate of genetic gain should be observed. The yearly rate of genetic gain of ginning out-turn was of 0.0647 %, and 0.104 % in Garoua and in Maroua, respectively (Table 7).

There was no significant genetic gain on the number of bolls per m^2, average boll weight and seed unit mass (Table 7).

Table 7. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Yield and its components.

	Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar											
Cropping conditions	Boll nbr m^{-2}†		Average boll weight (g)		Seed mass index (g)‡		Seed cotton yield (kg ha^{-1})		Ginning out-turn (%)		Fiber yield (kg ha^{-1})	
	Estimates ($x10^{-3}$)	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates*	*Pvalue*
G0: Garoua planted June 14	11.4 (±84.5)§	0.89 ns¶	-5.2 (±6.2)	0.41 ns	-0.97 (±7.9)	0.90 ns	-3.6 (±2.8)	0.20 ns	78.4 (±31.2)	0.019 *	2.9 (±1.2)	0.029 *
G1: Garoua planted June 27	-9.0 (±84.5)	0.92 ns	3.6 (±6.2)	0.57 ns	-6.1 (±7.9)	0.45 ns	3 (±2.8)	0.28 ns	49.6 (±31.2)	0.13 ns	4.8 (±1.2)	0.0008 ***
G2: Garoua planted July 11	-69.7 (±84.5)	0.42 ns	5.4 (±6.2)	0.39 ns	-1.8 (±7.9)	0.82 ns	0.32 (±2.8)	0.91 ns	66.1 (±31.2)	0.045 *	2.1 (±1.2)	0.096 ns
(G0+G1+G2)/3: Garoua mean	*-22.4 (±60.3)*	*0.71 ns*	*1.3 (±4.2)*	*0.76 ns*	*-3.0 (±5.8)*	*0.61 ns*	*-0.097 (±1.7)*	*0.95 ns*	*64.7 (±30.2)*	*0.042 **	*3.3 (±0.83)*	*0.0006 ****
G2-(G0+G1)/2 contrast	-70.9 (±88.9)	0.43 ns	6.2 (±6.9)	0.38 ns	1.7 (±8.1)	0.83 ns	0.62 (±3.3)	0.85 ns	2.1 (±12)	0.87 ns	-1.7 (±1.4)	0.24 ns
Maroua planted July 6	39.3 (±84.5)	0.65 ns	-	-	-0.73 (±7.9)	0.93 ns	1.7 (±2.8)	0.54 ns	104 (±31.2)	0.0028 **	2.3 (±1.2)	0.072 ns

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
†Number of cotton bolls per m^2
‡ Average mass of 100 seeds (g/100 units).
§ Values in parenthesis are standards errors of the slope.
¶ ns, non significant at the 0.05 probability level.

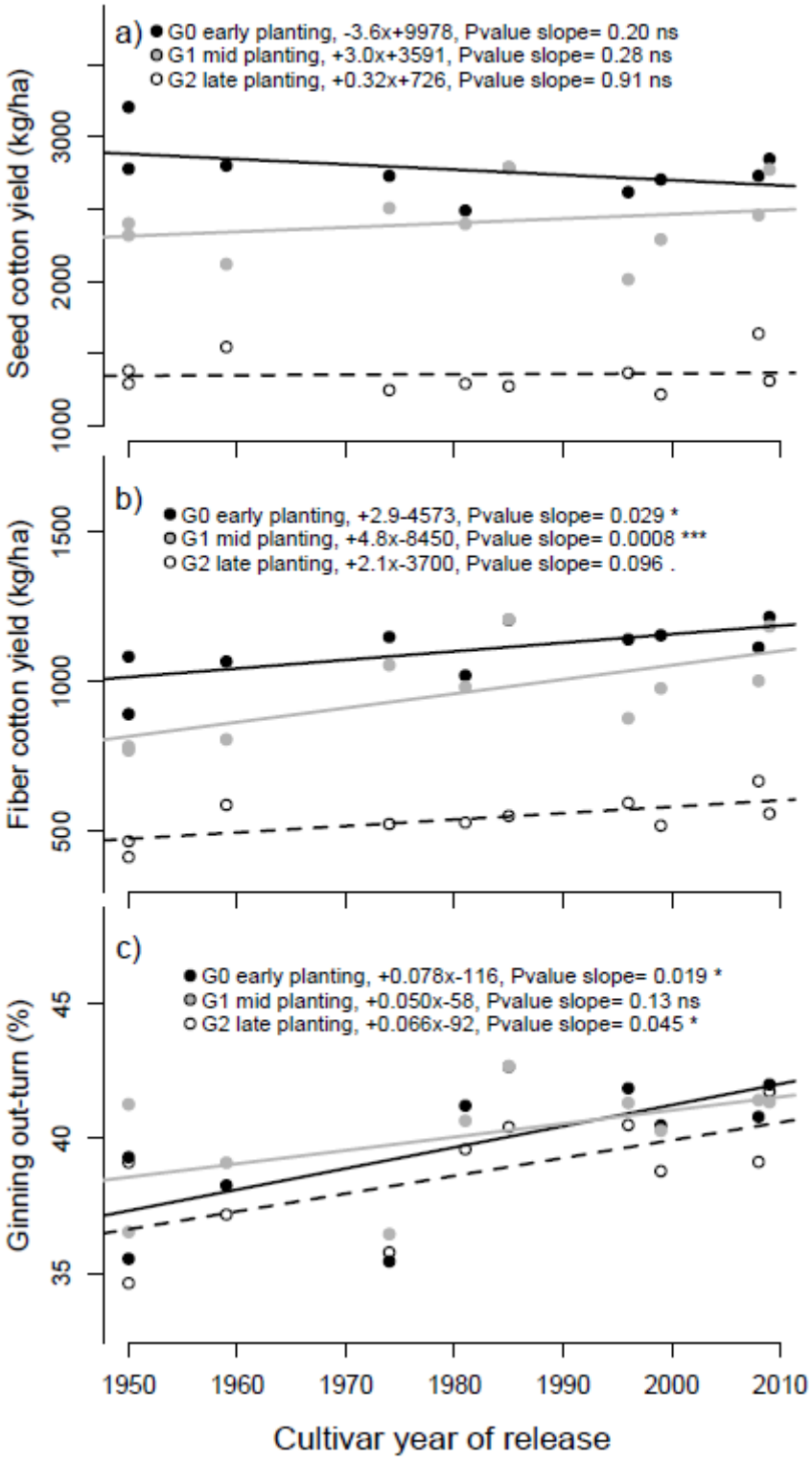

Figure 16. Seed and fiber yields (kg ha^{-1}), and ginning out-turn (% of fiber) regressed on the year of release of cotton cultivars in Garoua (Cameroon) according to the planting date.

Fiber yield was significantly improved only in early planting G0 and G1, while ginning out-turn was significantly improved only in G0 and G2 (Figure 2b and 2c). No interaction between year of release and planting date was significant, though. G0 was planted on June 14, G1 on June 27, and G2 on July 11 2012.

3.2. Fiber quality

Figure 17 shows some differences between rates of genetic gain of fiber upper half mean length (UHML) observed with different planting dates. This is confirmed by highly significant contrast (Table 8, "G2-(G0+G1)/2 contrast", *Pvalue= 0.0058*). On UHML, no genetic gain was observed in early planting and mid-planting whereas a significant decrease was found in late planting, in Garoua (-0.0034 mm year^{-1}). Likewise, Table 8 shows significant differences between cropping conditions in Garoua in the rate of genetic gain for the short fiber index, uniformity index and strength. In good conditions, no genetic improvement was observed for these variables whereas in late planting, short fiber index, uniformity index and strength, showed a yearly genetic gain rate toward decreased quality; 0.015 %, - 0.034 %, -0.054 g tex^{-1}, respectively. Fiber elongation did not significantly change. Table 8 shows that no evolution was observed on these variables of fiber quality, in suboptimal conditions, in Maroua. Finally, Table 8 shows that in the non-limiting conditions of the greenhouse, length, uniformity index and strength were improved by breeding at a yearly rate of 0.10 mm, 0.070 %, and 0.11 g tex^{-1}, respectively.

Table 9 shows that in all the field conditions, no genetic gain was observed on fiber standard fineness (smaller is better), maturity ratio, percentage of fibers, micronaire index, brightness and yellowness. However, in the non-limiting conditions of the greenhouse, a genetic improvement was observed on the fiber standard fineness, and its maturity ratio as showed by yearly rates of –0.8 mtex, 0.37 %, respectively. In the greenhouse, no genetic improvement was observed on micronaire index, brightness and yellowness index.

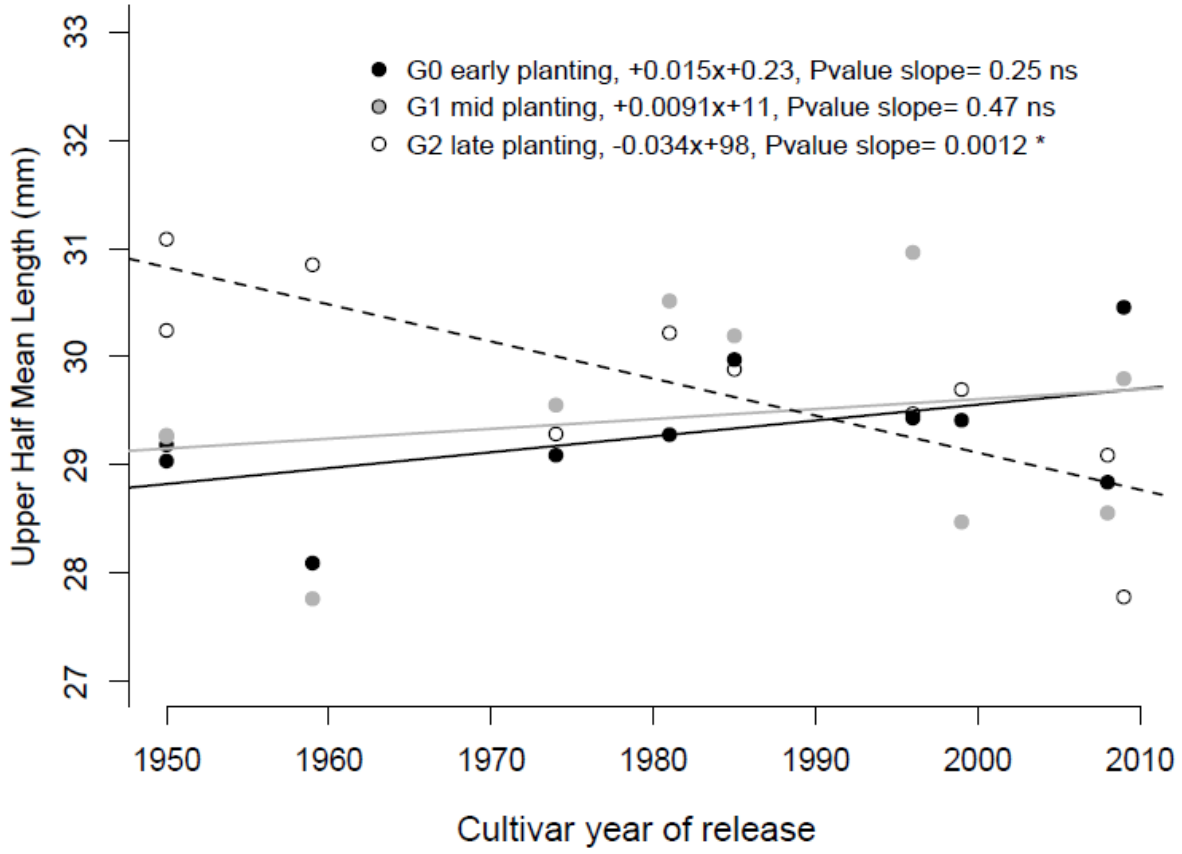

Figure 17. Upper half mean length (mm) regressed on the year of release of cotton cultivars in Garoua (Cameroon), according to planting date.

Yearly genetic gain was not significant for early planting dates (G0 and G1), while a significant yearly loss was observed on late planting condition (G2). Test for interaction between year of release and planting date confirmed significantly different rates of genetic gain. G0 was planted on June 14, G1 on June 27, and G2 on July 11 2012.

Table 8. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Fiber quality part I.

Cropping conditions	Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar									
	Length (mm) †		Short fiber index (%)‡		Uniformity index (%)§		Strength (g/tex)		Elongation (%)	
	Estimates (x10-3)	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*
G0: Garoua planted June 14	*14.7 (±12.5) ¶*	*0.25 ns#*	*-2.3 (±5.2)*	*0.67 ns*	*15.5 (±9.4)*	*0.11 ns*	*33.4 (±17.5)*	*0.069 ns*	-4.2 (±5.6)	0.46 ns
G1: Garoua planted June 27	*9.1 (±12.5)*	*0.47 ns*	*-4.3 (±5.2)*	*0.41 ns*	*10.5 (±9.4)*	*0.28 ns*	*23.3 (±17.5)*	*0.20 ns*	-5.6 (±5.6)	0.33 ns
G2: Garoua planted July 11	*-34.3 (±12.5)*	*0.012 **	*14.8 (±5.2)*	*0.0089 ***	*-34.3 (±9.4)*	*0.0013 ***	*-54.4 (±17.5)*	*0.0048 ***	6.4 (±5.6)	0.26 ns
(G0+G1+G2)/3: Garoua mean	-3.5 (±7.3)	0.64 ns	2.7 (±3.0)	0.37 ns	-2.8 (±5.9)	0.64 ns	0.75 (±10.2)	0.94 ns	*-1.1 (±3.6)*	*0.76 ns*
G2-(G0+G1)/2 contrast	-46.1 (±15.3)	0.0058 **	18.1 (±6.3)	0.009 **	-47.3 (±11.1)	0.0003 ***	-82.8 (±21.4)	0.0007 ***	11.3 (±6.4)	0.088 ns
Maroua planted July 6	-2.3 (±12.5)	0.85 ns	-0.06 (±5.2)	0.99 ns	0.88 (±9.4)	0.93 ns	9 (±17.5)	0.61 ns	-2.5 (±5.6)	0.66 ns
Greenhouse	103 (±9.9)	$<10^{-4}$***	-	-	70.2 (±6.4)	$<10^{-4}$***	109 (±21)	0.0013 **	-0.81 (±5.9)	0.89 ns

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Fiber upper half mean length (UHML) (mm).
‡ Short fiber index : Fibers shorter than 0.5 inch) (%).
§ Uniformity of fiber length (ratio of mean length to UHML).
¶ Values in parenthesis are standards errors of the slope.
# ns, non significant at the 0.05 probability level.

Table 9. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Fiber quality part II.

Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar

Cropping conditions	Fineness std (mtex)		Maturity ratio (0-1)		Micronaire index		Brightness (%)		Yellowness index (%)	
	Estimates	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates (x10-3)*	*Pvalue*
G0: Garoua planted June 14	-0.045 (±0.20)†	0.82 ns‡	-0.11 (±0.76)	0.88 ns	-1.3 (±3.9)	0.73 ns	-0.26 (±16)	0.99 ns	-4.1 (±7)	0.57 ns
G1: Garoua planted June 27	-0.33 (±0.20)	0.10 ns	1.20 (±0.76)	0.13 ns	3.0 (±3.9)	0.45 ns	-3.2 (±16)	0.84 ns	1.7 (±7)	0.81 ns
G2: Garoua planted July 11	0.28 (±0.20)	0.16 ns	-0.76 (±0.76)	0.33 ns	-0.78 (±3.9)	0.84 ns	-9.5 (±16)	0.56 ns	2.9 (±7)	0.68 ns
(G0+G1+G2)/3: Garoua mean	*-0.032 (±0.11)*	*0.78 ns*	*0.11 (±0.44)*	*0.8 ns*	*0.29 (±2.2)*	*0.90 ns*	*-4.3 (±10.3)*	*0.68 ns*	*0.18 (±4.5)*	*0.97 ns*
G2-(G0+G1)/2 contrast	0.47 (±0.24)	0.061 ns	-1.30 (±0.93)	0.17 ns	-1.6 (±4.7)	0.74 ns	-7.8 (±18.2)	0.67 ns	4.1 (±8)	0.61 ns
Maroua planted July 6	-0.13 (±0.20)	0.53 ns	0.16 (±0.76)	0.84 ns	-0.95 (±2.8)	0.75 ns	6.3 (±16)	0.70 ns	-3.6 (±7)	0.61 ns
Greenhouse	-0.80 (±0.19)	0.004 **	3.70 (±0.94)	0.0053 **	13.0 (±7.0)	0.11 ns	-19.2 (±23.1)	0.44 ns	-1.4 (±8.8)	0.88 ns

** Significant at the 0.01 probability level.
† Values in parenthesis are standards errors of the slope.
‡ ns, non significant at the 0.05 probability level.

Table 10. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Aerial development and growth.

Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar

Cropping conditions	Number of vegetative branches		Node of first fruiting branch (n° of the node)		Emergence to Anthesis (GDD)		log10(phyllochron 60DAP) (x10^{-3})		Max number of nodes†		Heigth max (cm)‡		Age at 1st open boll (GDD§)	
	Estimate (x10-3)	*Pvalue*	*Estimate (x10-3)*	*Pvalue*	*Estimate*	*Pvalue*	*Estimate (x10-3)*	*Pvalue*	*Estimate (x10-3)*	*Pvalue*	*Estimate*	*Pvalue*	*Estimate*	*Pvalue*
G0: Garoua planted June 14	-7.7 (±4.9) ¶	0.13 ns#	3.7 (±4.9)	0.46 ns	0.31 (±0.32)	0.34 ns	-0.66 (±0.48)	0.18 ns	24.7 (±17.7)	0.18 ns	-0.04 (±0.11)	0.71 ns	0.021 (±0.43)	0.96 ns
G1: Garoua planted June 27	9.5 (±4.9)	0.067 ns	10.5 (±4.9)	0.040 *	0.32 (±0.32)	0.33 ns	-0.28 (±0.48)	0.57 ns	15.7 (±17.7)	0.38 ns	0.14 (±0.11)	0.19 ns	0.25 (±0.43)	0.56 ns
G2: Garoua planted July 11	-4.9 (±4.9)	0.33 ns	11.9 (±4.9)	0.023 *	0.51 (±0.32)	0.13 ns	-0.13 (±0.48)	0.79 ns	-7.1 (±17.7)	0.69 ns	0.068 (±0.11)	0.53 ns	0.60 (±0.43)	0.17 ns
(G0+G1+G2)/3: Garoua mean	*-1.0 (±3.3)*	*0.75 ns*	*8.7 (±3.5)*	*0.019 **	*0.38 (±0.24)*	*0.13 ns*	*-0.36 (±0.28)*	*0.21 ns*	*11.1 (±10.5)*	*0.30 ns*	*0.057 (±0.062)*	*0.37 ns*	*0.29 (±0.27)*	*0.29 ns*
G2-(G0+G1)/2 contrast	-5.7 (±5.5)	0.31 ns	4.8 (±5.1)	0.36 ns	0.19 (±0.32)	0.55 ns	0.34 (±0.59)	0.56 ns	-27.3 (±21.3)	0.21 ns	0.016 (±0.13)	0.90 ns	0.47 (±0.5)	0.36 ns
Maroua planted July 6	5.0 (±4.9)	0.32 ns	16.3 (±4.9)	0.0027 **	-0.36 (±0.32)	0.28 ns	-0.02 (±0.48)	0.96 ns	29.2 (±17.7)	0.11 ns	0.15 (±0.11)	0.18 ns	1 (±0.43)	0.022 *
Greenhouse	-	-	-	-	-	-	0.15 (±1.4)	0.92 ns	-	-	-	-	-	-

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† Maximum number of node on the main stem.
‡ Maximum plant main stem height (cm).
§ GDD: growing degree day in base 13°C.
¶ Values in parenthesis are standards errors of the slope.
# ns, non significant at the 0.05 probability level.

3.3. Development and growth

3.3.1. Aerial development and growth

There was a significant difference between G0 and G1 on the rate of genetic gain of the number of vegetative branches (Table 10). Nonetheless, no genetic gain was observed for that number for each single cropping condition alone. For all other variables of the aerial development and growth, Table 10 shows no difference between cropping conditions in Garoua. Table 10 only shows genetic gain on the number of the node of insertion of the first fruiting branch on the main stem, the rate was of 0.0087 and 0.016 nodes year^{-1}, in Garoua, and in Maroua, respectively.

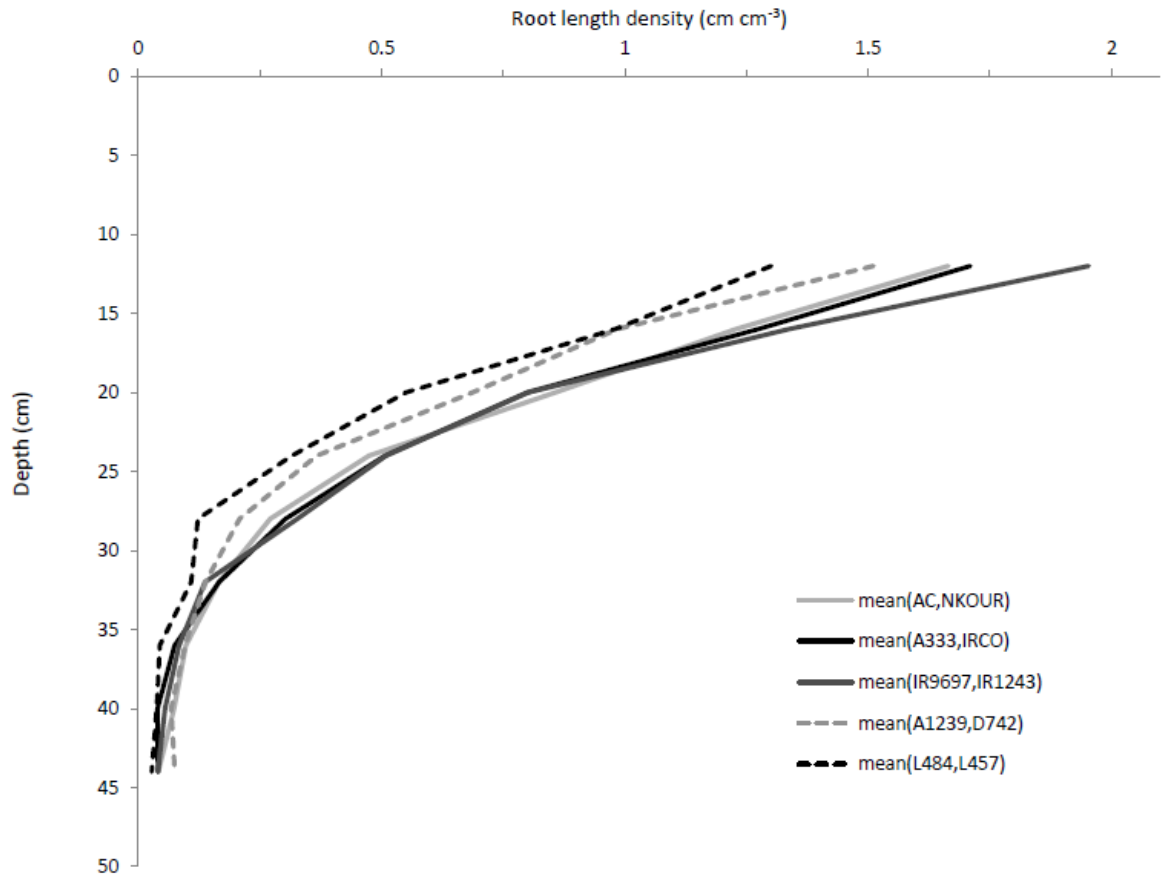

Figure 18. Cotton root length density (cm3 root cm-3 soil) as a function of soil depth in a phytotron, Montpellier, France, 2012.

Average profiles per coupled cultivars from oldest (AC, NKOUR) to most recent (L484, L457). No error bar are showed, all of them are wider that distance between curves.

3.3.2. Shoot and Root development in phytotron

In phytotron and rhizoboxes conditions, estimated values of root (Figure 18, Table 11) and shoot (Table 11) characteristics allowed us to evaluate the rate of genetic gain on each characteristic measured.

At 17 DAP, aerial biomass between cultivars was not statistically different, despite the highest biomass being more than twice the smallest (AC versus L457, respectively). This was probably due to the small size of each experimental unit. However, the plant leaf area of cultivar AC (released in 1950) was significantly higher than L484 (2008), similar to what we observed in the field. There was a significant decrease in aerial biomass and leaf area at 17 DAP by 7.7 mg plant^{-1} and 1.5 mg plant^{-1} each year, respectively (Table 11).

There was no significant difference between root length density (RLD) profiles from 10 to 46 cm (Figure 18). The four most recent cultivars A1239 (1996), D742 (1999), L484 (2008) and L457 (2009) seemed to have smaller RLD compared to the six older ones released between 1950 and 1985. Between 10 and 46 cm depth, RLD of the six oldest varieties were 31 % higher than the four most recent but it was not statistically different.

At 17 DAP, no significant difference between cultivars was observed on root biomass, length of the longest root (indicated by the root speed of growth), RLD, percentage of root-free zones. Nonetheless, important disparities were observed between cultivars. The RLD ranged from 0.62 and 0.63 cm cm^{-3} for cultivars released in 1950 and 1981, to 0.36 cm cm^{-3} for the most recently released cultivar (2009). Root distances were significantly increased (0.043 mm year^{-1}), while PRER for nutrients (r = 0.5 cm) was significantly reduced (0.069 % year^{-1}). Cultivars AC, A333, A1239, D742 had wider root angle compared to L484 and NKOUR. Root angle seemed to be independent of the YR.

Ratio of leaf area to RLD and leaf area to PRER (for both migration distances) were significantly higher for AC (1950) compared to L484 (2008). For migration distance of 5 cm, the two most recently bred cultivars had a smaller ratio of leaf area to PRER than AC (1950). The ratio of leaf area to PRER of nutrients (r = 0.5 cm) was significantly reduced (0.019 m^2 %$^{-1}$ year^{-1}).

This shows that in the phytotron experimental conditions, breeding efforts tended to reduce the size of root system and aerial parts. However, this reduction was higher for aerial parts than for the roots.

Table 11. Estimates of 10 cotton cultivars root characteristics and related rate of genetic progress measured in a phytotron, Montpellier (France), in 2012.

Cultivars	Name	AC	NKOUR	A333	IRCO	IR9697	IR1243	A1239	D742	L484	L457	Genetic progress	
	Year of release	1950	1950	1967	1974	1981	1985	1996	1999	2008	2009	Slope	*P-value*
Aerial global	Biomass per plant (mg)	1512	1006	1310	1109	1440	1345	1132	1065	745	694	**-7.7**	**0.017***
	Leaf area per plant (cm²)	327 a†	198 ab	254 ab	231 ab	301 ab	281 ab	235 ab	213 ab	151 b	159 ab	**-1.5**	**0.015***
Roots global	Biomass per plant (mg)	272	204	221	208	286	251	242	180	155	147	-1.2	0.088
	Root angle (°)	139 a	88 c	132 a	110 abc	111 abc	123 ab	139 a	137 a	98 bc	120 ab	0.066	0.68
	Speed growth (cm/day)	3.0	3.2	3.2	3.3	3.4	3.3	3.2	3.7	3.1	3.3	0.0035	0.50
Roots	Root length density (cm/cm3)	0.46	0.62	0.50	0.59	0.63	0.53	0.50	0.42	0.42	0.36	-0.0025	0.059
(depths 10-46cm)	Root-free zone (%)	40.3	34.0	35.2	26.4	35.2	41.7	34.7	36.1	42.4	39.6	0.063	0.38
	Avg distance between roots (cm)	1.85	1.79	1.91	1.95	1.81	1.84	1.94	1.97	2.04	2.23	**0.0043**	**0.026***
	PRER‡ (with r=5 cm) (%)	73.1	76.5	70.3	78.1	70.2	68.5	77.1	72.2	65.1	68.3	-0.094	0.14
	PRER (with r=0.5cm) (%)	13.4	17.0	14.4	16.8	17.5	14.7	14.2	12.2	11.8	10.0	**-0.069**	**0.041***
Ratios	Aerial/root biomass (g g^{-1})	5.65	5.05	5.93	5.38	5.09	5.51	4.75	5.95	4.89	4.81	-0.0079	0.112
	Leaf area/root length (cm² cm^{-1})	0.61 a	0.28 b	0.44 ab	0.36 b	0.43 ab	0.48 ab	0.4 ab	0.46 ab	0.28 b	0.42 ab	-0.0011	0.29
	Leaf area/PRER 5cm (m² $\%^{-1}$)	4.48 a	2.58 ab	3.61 ab	3.00 ab	4.31 ab	4.02 ab	2.99 ab	2.97 ab	2.20 b	2.33 b	**-0.019**	**0.020***
	Leaf area/PRER 0.5cm (m² $\%^{-1}$)	24.4 a	11.8 b	17.6 ab	14.3 b	17.7 ab	19.7 ab	16.3 ab	18.2 ab	11.5 b	17.0 ab	-0.043	0.27

* Significant at the 0.05 probability level.
† Cultivars with no common letter within the same line are significantly different at Tukey test 5%.
‡ Potential root extraction ratio: percentage of soil available for water or nutrients uptake

Table 12. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Radiation use components.

Cropping conditions	Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar																	
	Leaf number at 65 DAP†‡		Mean area of a leaf (cm2) at 65 DAP§		Leaf area index at 65 DAP		Leaf area index max		log10(SLA) at 65 DAP¶		RUE (g/MJ)#		Leaf pilosity		A††		GH2O‡‡	
	Estimates	*Pvalue*	*Estimates (x10-3)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates ($x10^{-3}$)*	*Pvalue*	*Estimates*	*Pvalue*
G0: Garoua planted June 14	-0.6 (±0.17)§§	0.0016 **	-129 (±99)	0.21 ns¶¶	-6.4 (±3.8)	0.1 ns	*-3 (±6.5)*	*0.65 ns*	-3.5 (±1.2)	0.0098 **	3.7 (±3.4)	0.29 ns	-12.9 (±6.7)	0.065 ns	-	-	-	-
G1: Garoua planted June 27	-0.3 (±0.17)	0.088 ns	-23.1 (±99)	0.82 ns	-3.3 (±3.8)	0.4 ns	*1.7 (±6.5)*	*0.8 ns*	-0.81 (±1.2)	0.52 ns	4.7 (±3.4)	0.19 ns	-19.9 (±6.7)	0.0064 **	-	-	-	-
G2: Garoua planted July 11	-0.069 (±0.17)	0.69 ns	22.8 (±99)	0.82 ns	1.8 (±3.8)	0.64 ns	-	-	-0.43 (±1.2)	0.73 ns	-4.1 (±3.4)	0.24 ns	-8.7 (±6.7)	0.2 ns	-	-	-	-
(G0+G1+G2)/3: Garoua mean	*-0.32 (±0.099)*	*0.0031 ** *	*-43.0 (±61)*	*0.49 ns*	*-2.6 (±2.5)*	*0.3 ns*	*-1.6 (±4)*	*0.69 ns*	*-1.6 (±0.9)*	*0.094 ns*	*1.4 (±2)*	*0.49 ns*	*-13.8 (±5.1)*	*0.013 **	-	-	-	-
G2-(G0+G1)/2 contrast	0.38 (±0.21)	0.076 ns	98.7 (±117)	0.41 ns	6.6 (±4.2)	0.13 ns	-	-	1.7 (±1.3)	0.19 ns	-8.3 (±4.1)	0.056 ns	7.7 (±6.3)	0.24 ns	-	-	-	-
Maroua planted July 6	-0.097 (±0.17)	0.57 ns	-79.6 (±99)	0.43 ns	-5.4 (±3.8)	0.17 ns	-3.4 (±7.8)	0.67 ns	-2.4 (±1.2)	0.067 ns	-2.5 (±3.4)	0.47 ns	-3.7 (±6.7)	0.58 ns	-	-	-	-
Greenhouse	-	-	-	-	-	-	-	-	0.071 (±0.40)	0.86 ns	-	-	-	-	13.7 (±34.8)	0.7 ns	0.26 (±0.74)	0.74 ns

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† DAP: days after planting.
‡Total number of leaves per plant at 65DAP.
§ Average area of one leaf at 65 DAP (cm^2).
¶ log of specific leaf area ($cm^2\ g^{-1}$).
# Radiation use efficiency (g of dry biomass MJ^{-1} photosynthetically active radiation intercepted).
†† Carbon dioxide assimilation rate ($\mu mol\ m^{-2}s^{-1}$).
‡‡ Stomatal conductance ($mmol\ m^{-2}\ s^{-1}$).
§§ Values in parenthesis are standards errors of the slope.
¶¶ ns, non significant at the 0.05 probability level.

3.4. Radiation use components

Interaction between planting dates and genetic improvement was not significant for any radiation use components in Garoua (Table 12). No genetic gain was observed on the LAI at 65 DAP, the LAI maximum, the specific leaf area at 65 DAP, and the RUE. The number of leaves was significantly reduced in Garoua at a yearly rate of -0.32 leaf. At Garoua also, leaf pilosity showed a genetic loss at a yearly rate of -0.014 point.

3.5. Biomass and its allocation

There was neither a significant genetic improvement of the maximum biomass measured at 120 DAP nor of the harvest index (Table 13).

Table 13. Rate of genetic progress as measured in different environments, and contrast in rates between the late (G2) and the earlier (G0, G1) planted plots in Garoua (Cameroon). Biomass and its allocation.

Yearly genetic gain estimated by linear regression of each cultivar mean on the year of release of the cultivar

Cropping conditions	Aerial biomass max at 120 DAP†		Harvest index	
	Estimates	*Pvalue*	*Estimates (x10^{-3})*	*Pvalue*
G0: Garoua planted June 14	-13.4 (±15.6)‡	0.40 ns§	-0.26 (±0.96)	0.78 ns
G1: Garoua planted June 27	-1.9 (±15.6)	0.91 ns	-0.12 (±0.96)	0.90 ns
G2: Garoua planted July 11	-12.4 (±15.6)	0.43 ns	1.2 (±0.96)	0.22 ns
(G0+G1+G2)/3: Garoua mean	*-9.2 (±9.8)*	*0.36 ns*	*0.28 (±0.56)*	*0.63 ns*
G2-(G0+G1)/2 contrast	-4.8 (±18.2)	0.79 ns	1.4 (±1.2)	0.24 ns
Maroua planted July 6	-10.0 (±15.6)	0.53 ns	0.53 (±0.96)	0.58 ns

† DAP: days after planting.
‡ Values in parenthesis are standards errors of the slope.
§ ns, non significant at the 0.05 probability level

4. Discussion

Our objectives were to evaluate and analyze the genetic improvement of yield and fiber quality of Cameroonian cotton cultivars, and to determine whether this genetic improvement was affected by the planting date and water availability conditions.

4.1. Genetic improvement of cotton fiber yield and quality

Breeding program has increased the fiber yield per hectare (Table 7) via an increase in ginning out-turn (3.9 to 6.2 % in 60 years, Table 7), while the seed cotton yield remained unchanged. The observed increase in fiber yield did not result from increased biomass production or increased harvest index (Table 13). Likewise, the other yield components studied have not been changed by breeding; there was no significant effect of the year of release (YR) on the number of bolls produced, the average boll weight, and the seed unit mass (Table 7). Many of these results were as expected since the breeders aimed at increasing the fiber yield, and the Sodecoton, the ginning out-turn. The exception was the seed cotton yield which unexpectedly did not show any improvement.

The range of seed cotton yield obtained in this study in Garoua in good conditions (Appendix 1) was higher than that obtained by Naudin et al. (2010) (1460 and 1220 kg ha^{-1} in North and Far North regions, respectively) and Sissoko et al. (2013). This was probably due to the optimal precipitation regime for early and mid-planting conditions in Garoua in 2012. However, our results for seed cotton yield in the other cropping conditions were similar to theirs. In the USA, over the last 40 years, the genetic improvement for cotton fiber yield has been found to range from 3.7 to 10.2 kg ha^{-1} $year^{-1}$ (Schwartz and Smith, 2008a). In Australia, Liu et al. (2013) observed a range of fiber yield gain from 7.0 to 18.3 kg ha^{-1} $year^{-1}$ over the whole cotton belt for early cultivars and recent ones, respectively. Also in Australia, Rochester and Constable (2015) observed genetic improvement of cotton fiber yield of 28.8 kg ha^{-1} $year^{-1}$ and of ginning out-turn (1 % every 7 years, approximately). Similarly, they found no change in harvest index. On the contrary, Rochester and Constable (2015) found increased aerial biomass (92 kg ha^{-1} $year^{-1}$) and seed cotton yield (21.5 kg ha^{-1} $year^{-1}$). Our study concluded to an increase of cotton fiber yield of 3.3 kg ha^{-1} $year^{-1}$ (Table 7). This genetic improvement is small compared to that obtained in the USA and in Australia. This is probably because cotton breeding in Cameroon is targeting less favorable growing conditions (poor soil fertility, harsh climate, no irrigation). Our results showed no improvement of seed cotton yield in Cameroon though this seemed possible. Indeed, in similar

conditions, breeding has improved yield of other important crops (corn in Nigeria (Badu-Apraku et al., 2013) and in Kenya (Beyene et al., 2015); soybean in Nigeria (Tefera et al., 2009); cowpea in Nigeria (Kamara et al., 2011)).

In addition, breeders increased the potential of cotton fiber quality (Tables 8 and 9). The UHML and UI were significantly increased by the YR in the non-limiting condition (Table 8). These fiber traits all responded the same way to the YR, this could be due to the positive genetic correlation between fiber length and strength found by Campbell et al. (2012). The potential fiber strength and standard fineness were also significantly improved by breeding (Tables 8 and 9). The maturity ratio depends on environmental conditions. In non-limiting conditions, breeding efforts enhanced these variables (Table 9). Some other fiber technical characteristics showed no effect of the YR. Indeed, the fiber elongation, the brightness and yellowness were not a priority for breeders as the range of value was already good enough. Similarly, the micronaire index showed no genetic improvement (Table 9) but already belonged to the good or premium ranges of values with no significant price discount.

Our results clearly showed that breeding has improved ginning out-turn, fiber yield, potential fiber length, and potential fiber strength. In Australia, Rochester and Constable (2015) also found increased fiber length and strength by the YR.

Breeders have succeeded in increasing cotton fiber yield, with better fiber quality potential. As a consequence, the Commonwealth Scientific and Industrial Research Organisation (CSIRO) has well ranked Cameroonian fibers. For example, on average over all cultivars used had an upper half mean length classified as long (> 28.2 mm, Appendix 1). The uniformity index was already ranked as high (> 83%, Appendix 1) and reached very high (> 85%) according to the genetic gain observed in non-limiting conditions (Table 8). The fiber fineness was average to coarse (175 to 200 and 200 to 230 mtex, respectively; Appendix 1). Cameroonian fibers were mature (80.5 to 89.1 %, Table 9 and Appendix 1) and strong (30-33 m tex^{-1}, Tables 8 and Appendix 1).

4.2. Genetic improvement of morpho-physiological traits of cotton

The phyllochron and the duration from emergence to anthesis, or to first open boll showed no effect of the YR (Table 10). This was probably due to the absence of breeding effect on temperature responses of developmental processes for most of the crops, as reviewed by Parent and Tardieu (2012). Despite a higher node of insertion of the first fruiting branch with the same phyllochron, duration from emergence to anthesis remained unchanged (Table 10).

Recently bred cotton plants showed leaves with same thickness at the beginning of anthesis (Table 12). Likewise, we did not find any change in stomatal conductance, net photosynthesis, and in radiation use efficiency (Table 12). Bunce (2011) also found that sweet corn showed no evolution of stomatal conductance over different breeding eras. He found a significant difference between photosynthetic carbon dioxide assimilation rates of different eras; however, they did not result in any long term enhancement. Conversely, Cornish et al. (1991) found that Pima cotton photosynthesis was affected by breeding. This was probably because the latter aimed at high yield in very hot temperature, therefore targeting leaf cooling traits.

At a very early stage of development, recently bred cultivars showed decrease in both aerial and root biomass (Table 11) with unchanged shoot to root ratios except for the ratio of leaf area to the PRER of water (r = 5 cm). In addition, we observed an increased distance between roots leading to decrease in the potential root extraction ratio of nutrients (Table 11). These results could be explained by the absence of root traits measurements in the breeding process. Nonetheless, since breeding selected best plants in rainfed conditions, we expected an increase in root soil occupation leading to plants with higher water stress avoidance (Tardieu, 2013). In our experimental conditions, RLD ranged from 0.36 to 0.63 cm cm^{-3} on average on the depths between 10 and 46 cm, consistent with the literature (McMichael et al., 1996; Prior et al., 1994; Schwab et al., 2000; Shein and Pachepsky, 1995; Zamora et al., 2007; Zhang et al., 2006). We did not find any genetic improvement of root speed of growth (Table 11). Cook and Elzik (1992) found that rapid root-system establishment could improve drought tolerance and fiber yields in regions subjected to limited or poorly distributed rainfall conditions. This suggests that new cultivar showed reduced vigor at early stage of development, and did not show improved drought traits either.

4.3. Interaction between genetic improvement and cropping conditions

Interaction between genetic improvement and cropping conditions was significant only for fiber quality parameters (Tables 8 and 9). They did not affect the genetic improvement rate for yield components and yield (Table 7), development and growth (Table 10), radiation use (Table 12), and biomass and harvest index (Table 13). In contrast, Liu et al. (2013) found significant interaction between cropping management and genetic improvement on cotton yield in Australia. However, they cultivated irrigated cotton and the interaction was mainly due to higher rate of genetic gain on lint yield in cooler region than warmer, and resistance against disease. We found that in

unfavorable conditions, the quality of cotton fibers was decreased with the YR (Tables 8 and 9). Climate models predict more variability of rainy season pattern in sub Saharan Africa (Sultan et al., 2010). Therefore, breeding should try to increase plant flexibility for the maintenance of fiber quality under unfavorable conditions.

4.4. Perspectives and limitations

Despite very different field cropping conditions, we could only observe a small part of the existing climatic variability. In addition, first released cultivars were not cultivated according to our experiment cropping conditions when they were widely cultivated in Cameroon. This was especially true for the first two cultivars, Allen Commun and N'Kourala, originally cultivated without fertilizer or pesticides.

Complementary studies of roots in dry natural soil and at a later stage of development of cotton should be helpful to evaluate the impact of breeding on crop resistance to drought, as dry soil has been shown to enhance root development of cotton (Burke and Upchurch, 1995).

Cotton breeding strategy, as it is now, is not optimized for seed cotton yield improvement. A major shift in the ranking of breeding criteria is needed. Some physiological variables related to yield in water-limited conditions should be identified and targeted since it has already been demonstrated successful (metabolic response on peanut (Singh et al., 2014); greater RUE at the canopy level and high leaf assimilation rate on cereals (Fischer and Edmeades, 2010); leaf enhanced ribulose bisphosphate carboxylase activity on cotton (Plaut and Federman, 1991). These additional physiological traits indirectly linked to high yielding in drought conditions should be targeted as early as in generation F5 where there are still many different lines and already a population of plants.

Finally, some cotton crop models that include genetic parameters have successfully estimated yield and biomass (Gérardeaux et al., 2013; Ortiz et al., 2009; Zhang et al., 2008) and others, fiber quality (Wang et al., 2014; Zhao et al., 2013). Coupling these two kinds of models might enhance breeding efficiency.

5. Conclusion

Breeding program in Cameroon has succeeded in improving cotton fiber yield when the crop reaches physiological maturity before the end of the rainy season. In addition, most fiber technological characteristics showed improved potential. However, recently bred cultivars showed reduced flexibility to unfavorable conditions, with reduced vigor at early stage of development. Their root traits did not show enhanced drought adaptation. When rainy season ended before the end of cotton crop cycle, fiber length, uniformity and strength decreased with the year of release. This could be a problem in the context of climate change where increased variation in total amount of rainfall and length of rainy season are expected. There was not much improvement in potential root access to soil water. Most of the development and growth variables have also not changed except the leaf compartment which has fewer, thicker leaves. In order to increase both the cotton yield and maintain a high level of fiber quality, breeding efforts have to be maintained but should include the impact of climate change. This could aid in creating cultivars whose growth and development are better adapted to drought and water logging. In order to achieve these goals, the development of a bioclimatic model coupling climate change, biomass production and quality could be useful.

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Transition

Additional ecophysiological analyses were performed in controlled water-limited conditions to study cultivar water-response mechanisms in detail. In order to do so, a subset of cultivars with the greatest phenological differences should be done. Consequently, principal component analyses followed by hierarchical clustering were performed for group of variables related to development and morphology. See Appendix 2 for the detailed methodology. The cultivars selected for further study were L484, AC, IRCO and L457.

Drought adaptation morpho-physiological traits

This chapter was adapted from Loison, R., Audebert, A., Debaeke, P., and Gérardeaux E. Morpho-physiological traits conferring drought adaptation among cotton genotypes in Cameroon. In preparation for Journal of Agronomy and Crop Science.

HIGHLIGHTS

- *We compared adaptation to water deficit conditions of 4 cotton cultivars from different years of release in Cameroon.*
- *The impact of water deficit conditions was similar in greenhouse and in the field.*
- *No significant yield differences between cultivars whatever the water status.*
- *L484 had the highest maintenance of RUE and WUE in water deficit conditions.*
- *L484 and L457 showed higher lint percentage compared to obsolete cultivars whatever the water status.*

ABSTRACT

In Cameroon, water shortage is the major abiotic factor limiting cotton (*Gossypium hirsutum L*) yield and lint quality. Understanding cotton physiological responses to water supply and their consequences on growth and development therefore provides insight into the problem of yield stagnation. The underlying strategies for yield maintenance under water deficit in Cameroon have not been well understood. The objective of this paper is to evaluate which ecophysiological traits could confer a good response to drought among a panel of cotton genotypes used in Cameroon. These genotypes were compared in field and greenhouse trials under potential and water-limited conditions (fraction of soil transpirable water range: 0.39 to 0.83). Water deficit had a negative impact on almost all the plant functions, both under field and controlled environments. The recent cultivar L484 bred for the driest production area responded quite differently from the other cultivars in this study. L484 had the fastest development, thickest leaves with the most chlorophyll and thus maintained the highest level of photosynthesis and transpiration per unit of leaf area in water-limited conditions. In these conditions, L484 had the highest radiation use efficiency and water use efficiency maintenances. However, despite the advances in cotton breeding in Cameroon, no significant improvement between old cultivars and recently released ones were found on biomass, harvest index and cotton yield across water conditions. The lint percentage was the only yield component significantly enhanced, irrespective of water status.

1. Introduction

Cotton (*Gossypium hirsutum L.*) is the world's primary fiber crop (Park et al., 2012) and is considered as "the backbone of the textile industry" (Chakravarthy et al., 2014). As a typical smallholder cash crop, it provides income to more than 10 million people in West and Central Africa (Baffes, 2004) where it is mainly produced in rainfed conditions (Sultan et al., 2010). In these regions, water shortage is the major abiotic factor limiting cotton yield and lint quality (Leblois et al., 2014; Riaz et al., 2013a). Moreover, climate change models forecast higher risks of droughts (Rizza et al., 2004) and higher variability in rainy season length in arid to semi-arid areas (Vrieling et al., 2013) which will likely cause large yield losses in sub-Saharan Africa (Cairns et al., 2012).

Northern Cameroon is one region which should be highly affected by climatic change (Cao et al., 2011; Gérardeaux et al., 2013; Leblois et al., 2014). This region produced about 5 % of total African lint between 2000 and 2012 (FAOSTAT, 2014). A clear positive correlation was observed on historical records between cotton yield and total rainfall of June (beginning of the crop cycle) (Sultan et al., 2010). According to these findings, 68 % of the climatic years from 1950 to 2013 could be considered as yield limiting (< 120 mm) and only 32 % as favorable to production (> 120 mm) (data from SODECOTON in Maroua, Cameroon). Cotton adaptation to water stress could be achieved through agronomic practices or breeding for drought resistant cultivars (Luo, 2010). In order to create such varieties, a breeding program was initiated in Cameroon in 1950 (Levrat, 2010). The main targets were: increased productivity (in terms of yield and lint percentage), adaptation to environment (rainy season), resistance to pests and diseases (bacteriosis), and fiber quality (Levrat, 2010). This methodology proved successful in improving cotton fiber quality (Dessauw and Hau, 2007; Gérardeaux et al., 2013). Seed cotton yields have gradually increased until the mid-1980s, peaking at around 1200 kg ha^{-1} (Deveze and Halley des Fontaines, 2005) but levelling off in the last 20 years (Cao et al., 2011). Recent varieties cultivated with the best management practices yield about 30–45 % more than older ones (Lançon et al., 1990), suggesting but not demonstrating a genetic improvement.

Genetic strategies for yield maintenance under water deficit have been extensively documented. Tardieu described four main strategies (Tardieu, 2013): a) *escape* which consists in adapting the plant cycle to the water availability period for instance ; since timing of stress event is critical for cotton yield and fiber quality (Snowden et al., 2014), a fast plant development should be targeted ; b) *avoidance* which consists in maintaining plant water status with transpiration through

more water uptake by deeper and thicker roots (Suji et al., 2012) or reducing plant transpiration through stomatal closure or by reduction in leaf area (Chaves et al., 2002) ; c) *growth maintenance* which consists in a high photosynthesis level maintenance with a large leaf compartment; d) preferential allocation to reproductive organs (high harvest index).

Understanding cotton physiological responses to water supply and their consequences on reproductive growth and yield component development would provide insight into global yield stagnation problem (Morison et al., 2008; Pettigrew, 2004). Although cotton breeding program obviously enhanced production in sub-optimal water conditions, the underlying strategies for yield maintenance under water deficit have never been thoroughly studied. Therefore, the objective of this paper is to evaluate which ecophysiological traits could confer a good response to drought among genotypes grown in Cameroon in the past or nowadays.

A conceptual framework of crop growth and development was attempted in order to support our choice of variables measured or computed (Figure 19). This framework relates cotton yield to biomass production and biomass to radiation and water use components.

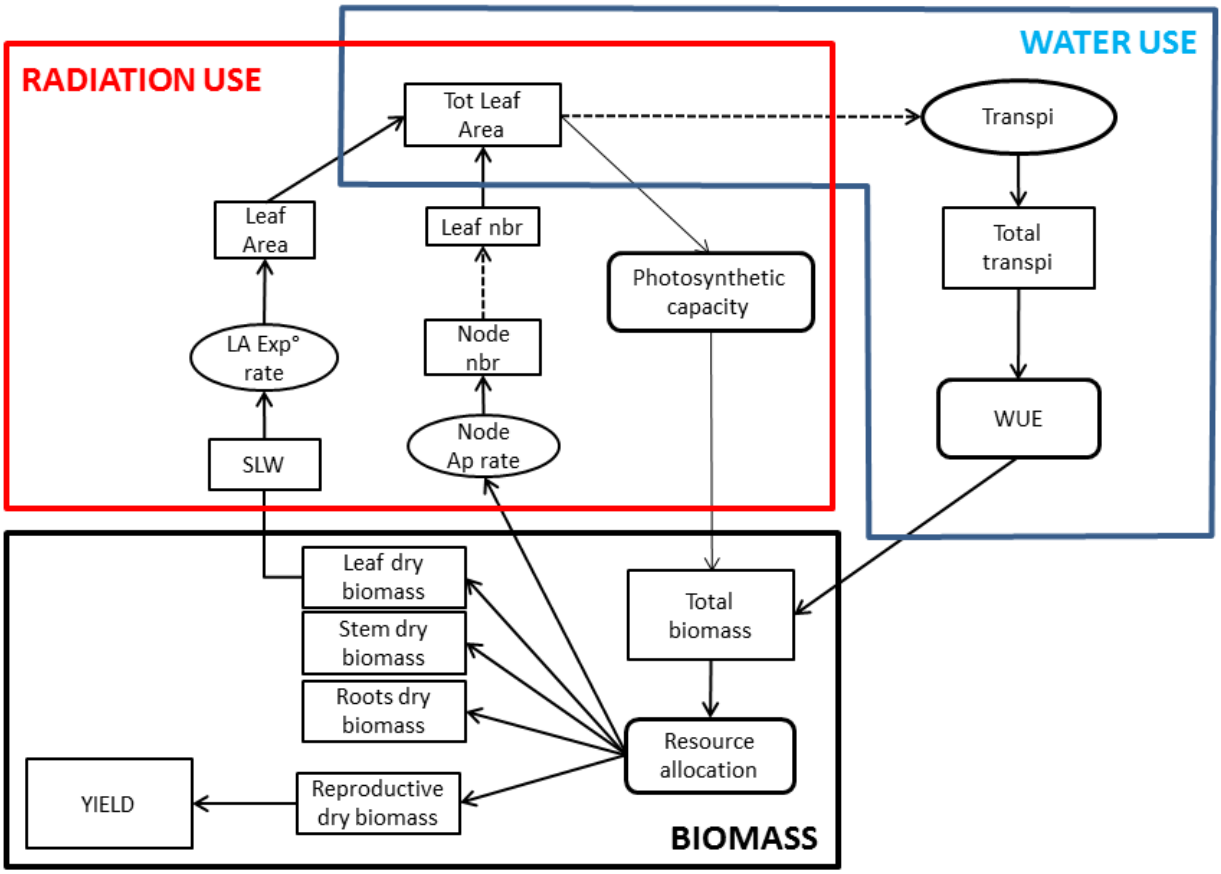

Figure 19. Conceptual model of radiation use, water use and plant biomass allocation.

The radiation use description focuses on light interception and transformation into biomass through photosynthesis. The main effective interception organ is the leaf compartment. It is dynamically described by the leaf number, dry mass, specific leaf weight (SLW). In addition, the average single leaf area depends on the leaf expansion rate. The total leaf area at a particular date is the product of the leaf number and the average single leaf area at that date. The chlorophyll contained in the total leaf area intercepts light every day and transforms it into biomass through photosynthesis. An indicator of the photosynthetic capacity is the radiation use efficiency (RUE), calculated as the ratio of top weight to the amount of photoactive radiation intercepted. The water use description focuses on water uptake and transformation into biomass through photosynthesis. The plant's water uptake organ is the root compartment. It is described by the dynamic change in root depth and soil occupancy. Water uptake by the root compartment is mainly transpired by the leaf compartment. Leaf area dynamic is important because when it increases, soil evaporation decreases and transpiration increases. Finally, biomass produced is allocated to new organs and is maintained throughout the crop cycle when no particular stress occurs or otherwise shed off. The harvest index is the ratio of cotton yield (seed and lint) to the top weight.

In order to compare radiation use efficiency (Monteith and Moss, 1977), water use efficiency (WUE) (Passioura, 1996) and efficient use of water (Blum, 2009) in drought conditions, a panel of cotton genotypes composed of widely cultivated cut edge cultivars with common parental and first cultivar used in Cameroon were compared in field and greenhouse trials under potential and water-limited conditions.

2. Material and methods

This study aimed at comparing the response of four cotton cultivars to several levels of water constraint. Cultivars were selected because they were widely cultivated in Cameroon (>100,000 ha each), and were cultivated at different periods. ALLEN COMMUN (AC) was grown between 1950 and 1956, IRCO 5028 (IRCO) between 1974 and 1988, IRMA L457 (L457) from 2009 for the North region with high water availability, and IRMA L484 (L484) from 2008 for the Far North region with low water availability (sub-Sahelian condition). Complementary level of analyze was possible. In the greenhouse, fine morpho-physiological measurements were done while in the field, morphological, biomass and yields variables measurements. Multiple cropping conditions in the

field and plant management in the greenhouse were used in order to create several levels of water constraint.

2.1. Experimental designs

2.1.1. In the field: four cultivars in nine crop management conditions

Nine crop management conditions defined by rainfall onset and pattern, soil property, planting date and level of fertilization (linked to planting date and location) in 2012 and 2013 in North and Far North regions of Cameroon were used in this study. In Maroua (10° 39′ N, 14° 25′ E, and altitude: 380 m), in Far North region, rainfalls are more limited compared to Soukoundou (9° 50′ N, 13° 52′ E, and altitude: 365 m) and Garoua (9° 15′ N, 13° 28′ E, and altitude: 250 m) both located in North region.

The trials were designed as split plot design with two factors and three replicates in 2012, and four in 2013. The whole plot factor was the planting date with three levels in Garoua 2012, and two levels in Maroua 2012, Garoua 2013, and Soukoundou 2013 as described below. The subplot factor was the cotton cultivar with the four levels as described in section 2 (AC, IRCO, L457, and L484). In Garoua, G0 2012 was planted on 14 June, G1 2012 on 27 June, and G2 2012 on 11 July 2012, while in 2013, G0 2013 was planted on 8 July, and G1 2013 on 22 July 2013. In Maroua, M0 was planted on 6 July, and M1 2012 on 19 July 2012. In Soukoundou, S0 2013 was planted on 4 July and S1 2013 on 18 July 2013. Levels of fertilization followed the recommendation of Sodecoton (Cameroonian cotton Development Company) according to planting date and location. General fertilizer (NPKSB 22-10-15-5-1 %) was first applied just after thinning at 200, 150, 100, 200,100, 200, 100, 200, and 100 kg ha^{-1} in G0 2012, G1 2012, G2 2012, M0 2012, M1 2012, G0 2103, G1 2013, S0 2013, and S0 2013, respectively. A supplemental amount of 23 kg ha^{-1} of urea (46 % urea) was applied at ridging in G0 2012, G1 2012, G0 2013, G1 2013, S0 2013, and S1 2013. Pests were controlled with recommended insecticides under rainfed conditions.

In 2012, each unit plot size was 32 m^2 with five rows of 8 m whereas in 2013, there was 88 m^2 with eleven rows of 10 m. Texture of soil was loamy sand in Garoua, loam in Maroua, and sandy clay loam in Soukoundou. Soil depths were 2.0 m, 1.4 m, and 1.4 m in Garoua, Maroua, and Soukoundou, respectively. Previous crop was a fallow in Garoua and soybean in Maroua.

In 2012, soil was ploughed with tractor disks on 13 and 12 June in Garoua and Maroua, respectively. In 2013, soil was ploughed with tractor disks on 14 June and with cattle traction on 3 July. Plant density was 31250 plants ha^{-1} with a row width of 0.8 m in the all locations.

2.1.2. In the greenhouse: four cultivars in two levels of soil water

The greenhouse experiment was carried out at CIRAD in Montpellier (France) in 2013. Planting date was April 3. The experiment was arranged as a factorial randomized block design with two factors and four replications. The two factors studied were the cotton cultivar (4 levels: AC, IRCO, L457, L484) and the water status (two levels: control versus fraction of transpirable soil water (FTSW) maintained at 40 %). Each experimental unit was a single cotton plant in 18.5 liters pot (h30 cm x Ø30 cm). Total transpirable soil water was 6400 g (±90 g). The growing medium was commercial potting soil Neuhaus N°9 with pH=6 and water holding capacity of 80 % (ANGIBAUD & SPECIALITES; La Rochelle, France). Optimal fertilization was applied at planting with slow release fertilizer (Basacote Plus 6M; COMPO, Nanterre, France) homogeneously mixed with potting soil at 3.5 g l^{-1}. Air temperature was automatically adjusted for optimal cotton growth (30 °C daytime and 25 °C nighttime). Temperature was measured at several points of the crop canopy and was averaged over the greenhouse. A sodium light supply was provided from 7:00 to 9:00 am and 5:00 to 7:00 pm (100 µmol m^{-2} s^{-1}). A quantum sensor (LI190SB-L; Campbell Scientific; Logan, Utah, USA) was placed on top of the canopy to measure the photoactive radiation. Weather data were recorded hourly in a data logger (CR-10X; Campbell Scientific; Logan, Utah, USA).

2.2. Evaluation of water constraint

2.2.1. In the field: Water balance model

Climatic data were recorded hourly with synoptic weather stations (iMETOS, PESSL instruments GmbH, Weiz, Austria) installed on each experimental site less than 10 km from the field. Rainfall was recorded daily at less than 100 m from the field. In 2013, in Garoua, sixteen soil samples from 0 to 60 cm taken along the season were oven-dried for humidity determination and then compared to output from PROBE-W, a generic soil water balance model developed for tropical regions (Chopart and Vauclin, 1990). Based on a coefficient of determination of 0.83 (Appendix 3), we concluded that this model could be used reasonably for cotton water balance estimation in Northern Cameroon. Thus, soil water content was simulated by PROBE-W and a threshold of 59 % actual to maximum evapotranspiration (ET_a/ET_m) was considered for important water limitation in our study, equivalent to a FTSW of 0.4. Crop managements which experienced similar pattern of

water constraint were gathered into crop management groups (CMG) for further analysis (Figure 20).

CMG A gathered best rainfed crop management conditions (G0 2012 and G1 2012) were ET_a/ET_m remained above the important water limitation threshold all along the season. Likewise, CMG B gathered crop management which experienced moderate water limitation (G2 2012, S0 2013 and G0 2013) with ET_a/ET_m above threshold until 100 days after planting (DAP) approximately but with some water deficit between 73 and 85 DAP. Finally CMG C (G1 2013, S1 2013, M0 2012 and M1 2012) experienced important water limitation as soon as 60 DAP and a final one starting from 67 to 94 DAP. Average values of FTSW from 60 to 105 DAP (anthesis to physiological maturity period used in PROBE-W) were estimated at 0.83, 0.65 and 0.39 for CMG A, B and C, respectively.

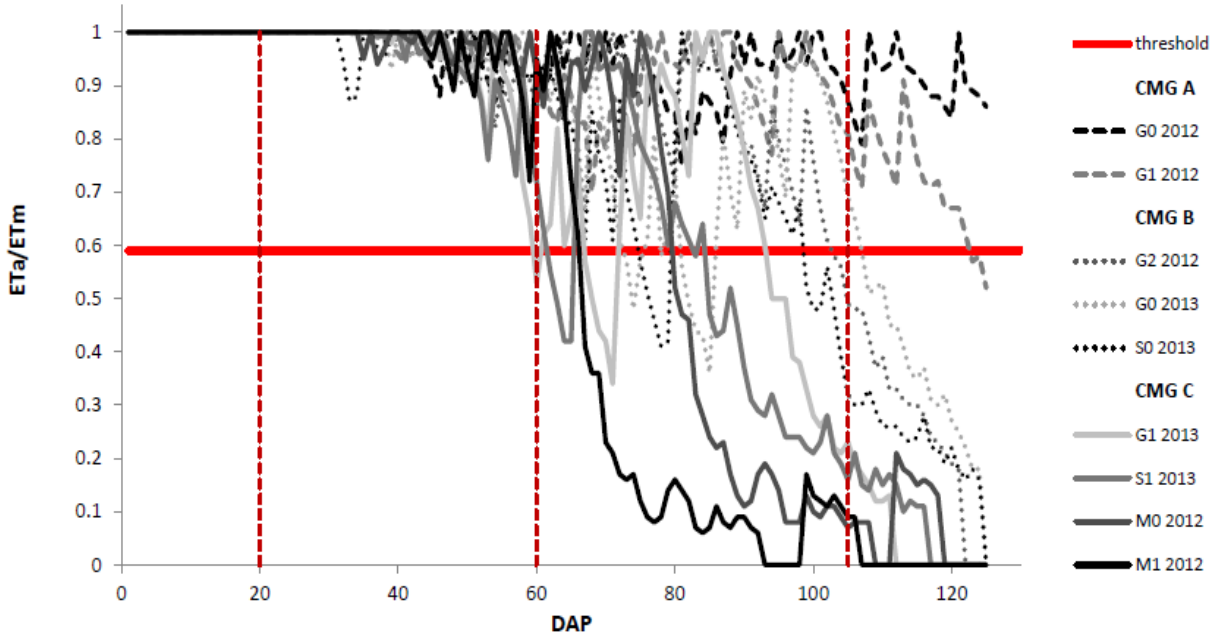

Figure 20. PROBE-W actual to maximal evapotranspiration (ETa/ETm) from 0 to 125 days after planting (DAP) by crop management.

Vertical dashed lines represent crop cycle used in PROBE-W (end of initial stage 20 DAP, end of development stage at 60 DAP, physiological maturity 105 DAP). Horizontal thick solid line represents the important water limitation threshold of ETa/ETm = 0.59. Dashed lines represent the best rainfed water conditions (Crop Management Group A [CMG A]). Dot lines represent conditions with moderate water limitation (CMG B). Solid lines represent early water-limited conditions (CMG C).

2.2.2. In the greenhouse: FTSW estimation

At 16 DAP right after thinning; pots were packed into white plastic bags to minimize water loss through soil evaporation. After 30 DAP, roots occupied the whole pot volume and water constraint was implemented by a dry out protocol. After a 3-5 days dry out, FTSW of water-limited plants was maintained at 0.4. Each day, pots were weighted and irrigated to reach a target weight. The FTSW 0.4 conditions were applied from 35 DAP to the end of experiment.

A preliminary drying out experiment gave us the relationship between FTSW and predawn leaf water potential (Ψ_{PD}) measured between 4:30 am and 5:00 am on cultivar L484. The relation obtained (R^2=0.87, Eq.1) was in accordance to previous study (Lacape et al., 1998). At FTSW = 0.4, corresponding Ψ_{PD} was -0.57 MPa indicating that plants were experiencing a severe water constraint.

$$FTSW = 1.174 * e^{-0.193 * \psi_{PD}} \quad (1)$$

From 35 to 60 DAP, all control pots were maintained above 0.75 FTSW and all water-limited plants were close to 0.4 FTSW (Figure 21).

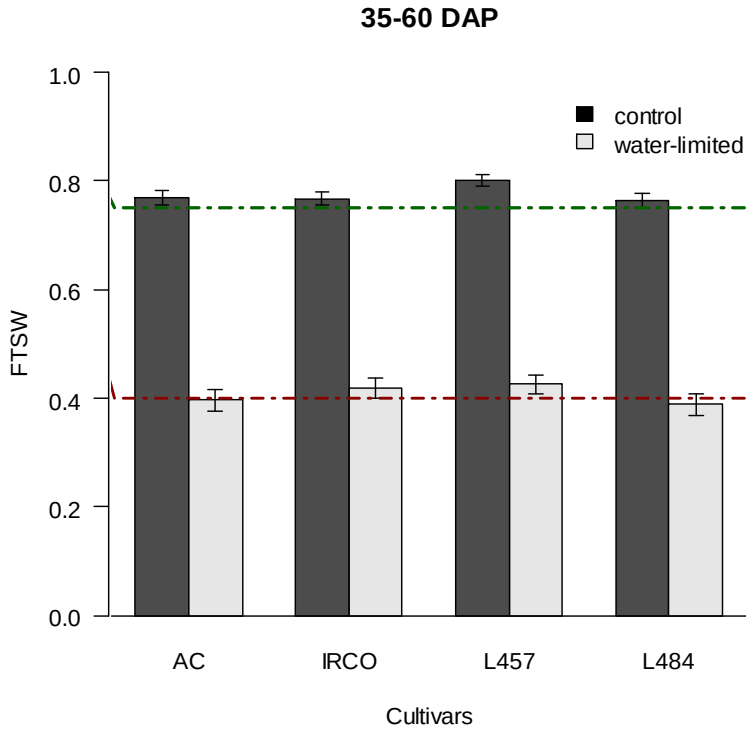

Figure 21. Greenhouse average fraction of transpirable soil water (FTSW) by cultivar and water status for the period from 35 to 60 days after planting (DAP).

Black is for control and grey for water-limited plants. Water-limited FTSW values were close to 0.4 for all cultivars, control were all above FTSW = 0.75.

2.2.3. The different water treatments

All 4 cultivars were found in each crop or greenhouse management conditions. At the end there were five levels of soil water availability (Table 14).

Table 14. List of crop management groups with detailed crop management conditions and corresponding water constraint intensity.

Water status groups	Management	Water constraint intensity
Greenhouse	control	0
CMG A	G0 2012 G1 2012	+
CMG B	G2 2012 S0 2013 G0 2013	++
CMG C	S1 2013 G1 2013 M0 2012 M1 2012	+++
Greenhouse	water limited	++++

2.3. Description of plant measurements

2.3.1. In the field

Each phenologic stage was identified as soon as 50 % of the plants in the observed line reached this stage. The main stages observed were: emergence (both cotyledons fully expanded), anthesis (1st open flowers) and first open boll. In each plot, five consecutive plants were tagged in 2012 and eight in 2013, and their number of nodes and main stem height were monitored regularly throughout the season. At harvest, these plants were mapped. The phyllochron was calculated as the ratio of the sum of growing degree days in base 13°C (GDD) to the number of nodes appeared during that period. Leaf area index (LAI) dynamics were recorded with a LICOR LAI-2200 (Li-Cor Inc., Lincoln, NE, USA). LAI was monitored nine times for G0 2013 and S0 2013, eight times for S1 2013, seven times for G1 2013, six times for G0 2012 and G1 2012, five times for M0 2012 and only twice for G2 2012 and M1 2012. Leaf hairiness is a proxy for leaf boundary layer thickness (Woolley, 1964; Wuenscher, 1970). It was measured at 90 DAP on five plants (Garoua 2012) and on ten plants (all other plots). A score from 0 (no hair) to 5 (maximum hairiness) was given to each leaf.

Destructive samplings of three plants in 2012 and five in 2013, were randomly done at 60 and 120 DAP, then top weight was determined. Cotton yield was measured on each plot on an area of 12.8 m^2 in 2012 and 53.8 m^2 in 2013. Lint yield was determined by multiplying cotton yield by the lint percentage. Lint percentage was measured by the Natural Fiber Technology and Characterization Laboratory (LTC, Montpellier, France). Harvest index was determined as cotton yield divided by top weight at 120 DAP.

2.3.2. In the greenhouse

Date of emergence and first true leaf appearance were noted to insure the homogeneity of plant development before water constraint application. The 24 h plant transpiration was measured daily. Day *d* transpiration was calculated as the difference between pot weight after irrigation on day *d-1* and pot weight before irrigation on day *d*. Total transpiration was calculated as the sum of daily transpiration from bag closure to the end of the experiment. The WUE was calculated as the ratio of top weight to total transpiration. Top weights were measured at thinning and at 60 DAP. Photosynthesis was measured twice on the 3rd youngest fully expanded leaf on the main stem at 37-38 and 57-58 DAP using a portable gas-exchange analyzer (GFS-3000; Heinz Walz GmbH, Germany). Measurements were done between 9:30 am and 11:00 am. The leaf surrounding volume was set at photosynthetic photon flux density of 1500 µmol m^{-2} s^{-1} and temperature of 30 °C, relative humidity 65 % and [CO_2] of 350 ppm. Assimilation rate (iA), stomatal conductance (g_s) and instant WUE (WUE_i) were calculated as previously described (Stuerz et al., 2014).

Allometric relationships between leaf dimension and area have been extensively used (Fideles Filho et al., 2010; Grimes and Carter, 1969). For each cultivar, the length of leaf vein localized on the left to the central vein of the upper side (*LVL*, in mm, vein #4 in Figure 1) was measured using a ruler and leaf area was assessed with a scanner (LI-3100-C, LI-COR Inc., Lincoln NE USA). A strong allometric relationship between one leaf area (*LA*, in cm^2) and its corresponding *LVL* was established on about 50 leaves per variety (Eq.2)

$$LA = \alpha * LVL^{\beta} \qquad (2)$$

Parameters α and β were respectively 0.00667 and 2.093 for AC (R^2= 0.97), 0.0147 and 1.972 for IRCO (R^2=0.97), 0.012 and 1.899 for L457 (R^2=0.96) and 0.00337 and 2.210 for L484 (R^2=0.96). Plant leaf number only considers leaves with *LVL* >30mm. Plant total leaf area at date *d* was calculated as the sum of each leaf area of the plant at date *d*. The average area of a single leaf was

calculated as the ratio of total leaf area to the total number of leaves of the plant. Plant total synthetized leaf area (*TSLA*) was defined for period of FTSW 0.4 as in Eq.3.

$$TSLA = leaf\ area_{62\,DAP} - leaf\ area_{35\,DAP} \quad (3)$$

Specific leaf weight (SLW) was calculated as the ratio of total leaf dry biomass to corresponding leaf area. Leaf dry weight was measured after drying leaves for 48 h at 80 °C.

From 5 total leaf area measurements per pot (two destructive ones at thinning and at 60 DAP and three nondestructive during crop cycle), a Hoerl nonlinear regression (Setiyono et al., 2008) was fitted (three parameters, R^2>0.997) to simulate the daily total leaf area course over the period. This power family kind of regression was already successfully used in daily estimation of LAI in field studies (data not shown).

Total intercepted photosynthetically active radiation ($\sum PAR_{int}$) depends on the coefficient of light extinction (*k*), LAI and PAR of each day (Eq.4). LAI was calculated with one plant soil occupancy of 0.5 m^2. PAR was hourly measured. For regular plant density, light interception coefficient (*k*) was considered constant (0.69) (Brodrick et al., 2013) and the maximum value of light interception that can be attained by the crop (εa_{max}) was set at 95 %. For a cotton canopy of LAI=3, 95 % of incident light is intercepted and CO2 assimilation is maximal (Stewart, 2009).

$$\sum PAR_{\text{int}} = \sum \varepsilon a_{\max} * (1 - e^{-k*LAI}) * PAR \quad (4)$$

The RUE was defined as the ratio of top weight produced to $\sum PAR_{int}$ over the same period (Monteith and Moss, 1977). It was calculated from thinning to 60 DAP.

2.4. Statistical analysis

The software R (R Core Team, 2014) with packages {agricolae} (Mendiburu, 2010) and {car} (Fox and Weisberg, 2010) were used for all statistical analysis. Type III analyses of variance were performed (Eq. 5, 6, 7 and 8). A down stepwise procedure was performed and led to Equation 5. For greenhouse study, results were also presented as percentages of control (water constraint effect on "potential" performance). Indeed, controls were averaged (Ray and Sinclair, 1998) and each variable was expressed as percentage of the average control (Eq.9). For percentages values, type III analyses of variance were also performed. Then, Tukey *post hoc* analyses at the 5 % significance level were done to examine possible differences between treatments.

In the field:

$$Y = C + CMG + C:CMG + Field + Field:C + Block(Field) + \varepsilon \quad (5)$$

$$\log(LAI) = sGDD + \log(sGDD) + CMG + sGDD:CMG + \log(sGDD):CMG + \varepsilon \quad (6)$$

In the greenhouse:

$$Y = C + WS + C:WS + Block + \varepsilon \quad (7)$$

$$Y = Date + C + WS + C:WS + Block + \varepsilon \quad (8)$$

$$Y_{\%\ of\ control} = C + Block + \varepsilon \quad (9)$$

C: cultivars
CMG: crop management group
Field: experimental field for specific year
Block(Field): block effect nested in *Field*
sGDD: sum of growing degree days in base 13 °C
WS: water status (water limited or control)

3. Results

3.1. Field

3.1.1. Phenology

There was no significant interaction between CMG and cultivars for all phenological durations and phyllochron (Table 15). The duration in GDD from planting to emergence, emergence to anthesis, and emergence to boll opening were not significantly different between cultivars. Cultivars AC and L484 had significantly shorter anthesis to boll opening compared to L457. Duration from emergence to boll opening significantly decreased with the intensity of water constraint (from CMG A to C) as the result of a shorter phase from anthesis to boll opening. Durations from planting to emergence and emergence to anthesis differed between crop management groups, CMG B resulting in the shortest periods. Cultivar AC had a significantly longer phyllochron than L484. CMG A forms more rapidly leaves than the other conditions as was indicated by phyllochron value.

Table 15. Field cotton phenology, phyllochron, leaf area index maximum, and node of insertion of the first fruiting branch by cultivar and crop management group (CMG).

Cultivars	CMG	†Planting-Emerg	†Emerg-Anthesis	†Anthesis-Boll opening	†Emerg-Boll opening	Phyllochron (GDD node^{-1})	‡LAI max	§N1BF
AC		83	775	623 ¶b	1398	58 a	2.9	5.6 b
IRCO		89	758	640 ab	1398	55 ab	2.8	5.6 b
L457		90	783	648 a	1428	56 ab	2.8	6.3 a
L484		78	772	624 b	1396	54 b	2.8	6.2 a
	A	99 a	789 a	712 a	1501 a	53 b	3.1 a	6.5 a
	B	57 b	758 b	646 b	1402 b	55 a	2.7 b	5.8 b
	C	101 a	775 ab	591 c	1366 c	57 a	2.8 b	5.9 b
Pvalue Cultivars		††*ns*	*ns*	**	*ns*	*ns*	*ns*	**
Pvalue CMG		***	ns	***	**	**	**	*
Pvalue CMG x Cultivars		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Phase duration expressed in growing degree days according to a base temperature of 13°C (GDD).
‡ Maximum leaf area index
§ node of insertion of the first fruiting branch
¶ Honest Significant Differences; values with a common letter are not different at Tukey 5 %
†† ns, non significant at the 0.05 probability level

3.1.2. Plant morphology, leaf area index and leaf area dynamics

There were significant interactions between cultivars and CMG for the maximum number of nodes on main stem (*Pvalue = 0.046**), the main stem maximum height (*Pvalue = 0.0018***), the internode length (*Pvalue = 0.013**) and the leaf hairiness (*Pvalue* <0.0001 ***) but not for the maximum LAI and the node of insertion of the first fruiting branch (N1BF) (Tables 15 and 16). Whatever the cultivars, the main stem maximum height was reduced by water deficit (from A to C) For CMG A and CMG C, the main stem maximum height was not influenced by cultivars. L457 was taller than IRCO and L484 in CMG B. All cultivars had the same maximum number of nodes on main stem when water was fully available (CMG A). In late water deficit (CMG B) and under the worst conditions (CMG C), L484 had a higher maximum number of nodes on main stem than older cultivars (IRCO and AC). Within each cultivar, internode length was the same for all CMG except for cultivar AC which had the smallest internode length in best conditions (CMG A). CMG B had the hairiest leaves for all cultivars. For all CMG, Cultivar AC had the hairiest leaves and IRCO and L484 always the least hairy ones. Recent cultivars (L457 and L484) had a higher N1BF than old ones. All cultivars had the same LAI at maximal development stage. Under good water conditions, higher N1BF and LAI maximum were observed. From overall Hoerl dynamic model, no significant LAI difference was observed between the four cultivars (data not shown).

3.1.3. Yield

There was no significant interaction between CMG and cultivar, and no effects of cultivar on cotton yield, top weight (60 and 120 DAP), lint yield and harvest index (Table 17). Yields, top weight at 120 DAP, lint percentage and harvest index significantly increased with the fulfillment of water requirement for cotton growth. Recent cultivars (L457 and L484) had higher lint percentage compared to older ones (AC and IRCO).

Table 16. Description of plant morphology in field experiment by cultivar, crop management groups (CMG) and their interaction.

Cultivars	Main stem height (cm)			Maximum # of node on main stem			Internode length (cm)			Leaf hairiness (0-5)		
	CMG A	CMG B	CMG C	CMG A	CMG B	CMG C	CMG A	CMG B	CMG C	CMG A	CMG B	CMG C
AC	117 †A ‡a	110 A ab	104 B a	25.6 A a	22.5 B b	20.9 C b	4.6 B bc	4.9 A a	5.0 A a	1.5 AB a	1.7 A a	1.3 B a
IRCO	121 A a	101 B b	102 B a	25.4 A a	21.4 B c	20.5 B b	4.8 A ab	4.7 A a	4.9 A a	0.5 B b	0.9 A c	0.7 AB b
L457	127 A a	114 B a	105 B a	25.9 A a	23.5 B a	21.3 C ab	4.9 A a	4.8 A ab	4.9 A a	0.7 B b	1.3 A b	0.8 B b
L484	120 A a	100 B b	102 B a	27.2 A a	22.7 B ab	22.1 B a	4.4 A c	4.4 A b	4.6 A b	0.2 B b	1.0 A c	0.8 A b
Pvalue Cultivars	***			**			***			***		
Pvalue CMG	***			***			***			***		
Pvalue CMG x Cultivars	**			*			*			***		

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† For each cultivar, CMG with a common upper letter do not differ at Tukey 5 %.
‡ For each CMG, cultivar with a common lower case letter do not differ at Tukey 5 %.

Table 17. Yield, lint percentage, top weight and harvest index from field experiments compared by cultivar and crop management groups (CMG).

Cultivars	CMG	Seed cotton yield (kg ha^{-1})	Lint (%)	Lint yield (kg ha^{-1})	Top weight 60†DAP (kg ha^{-1})	Top weight 120†DAP (kg ha^{-1})	Harvest index (%)
AC		1519	39.0 ‡b	554	1200	5098	28
IRCO		1392	34.4 c	543	1332	4855	27
L457		1485	40.7 a	625	1043	4789	28
L484		1498	40.4 a	609	1202	4346	32
	A	2697 a	39.8 a	1074 a	1283	6772 a	37 a
	B	1528 b	39.4 a	602 b	1223	4721 b	34 a
	C	906 c	37.5 b	358 c	1109	3941 b	23 b
Pvalue Cultivars		§*ns*	***	*ns*	*ns*	*ns*	*ns*
Pvalue CMG		***	***	***	*	***	**
Pvalue CMG x Cultivars		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Days after planting
‡ Honest Significant Differences at Tukey 5 %. CMG with a common letter do not differ at Tukey 5 %.
§ *ns*, non significant at the 0.05 probability level.

3.2. Greenhouse

3.2.1. Effect of water regime on radiation use components

There was no significant interaction between cultivar and water status concerning all the radiation use components (Table 18) except for instant CO2 assimilation rate (iA) (Figure 22, *Pvalue =0.042*).* Within control level, all cultivars had the same iA ranging from 28.2 to 30.1 µmol m^{-2} s^{-1}. Within water-limited level, L484 had a significantly higher iA (28.7 µmol m^{-2} s^{-1}) than other cultivars (ranging from 19.7 to 21.9 µmol m^{-2} s^{-1}) and was the only cultivar to maintain its iA under water constraint condition.

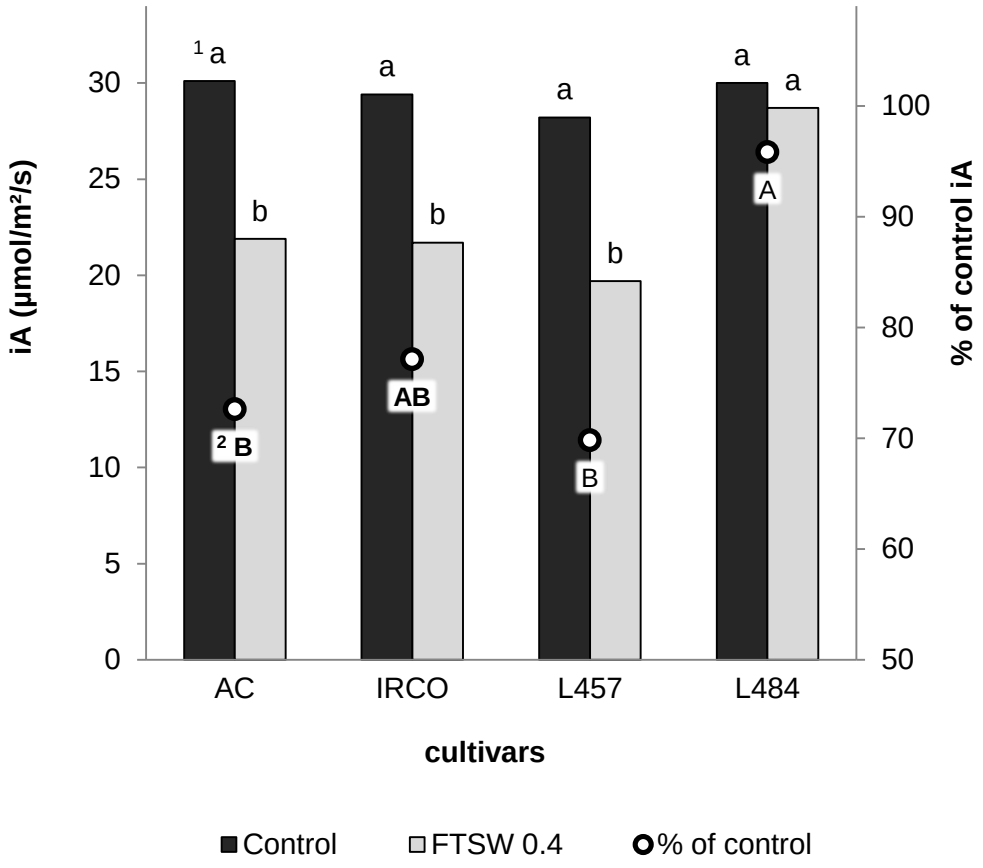

Figure 22. Average values of control, water-limited conditions and % of control for instant CO2 assimilation rate (iA).

Black is for control, grey for FTSW=0.4 and circle for % of control. Left axis for iA, right axis for % of control iA. Measurements were done on the third youngest leaf fully expanded on the main stem between 9:30am and 11:00am. The leaf surrounding volume was set at photosynthetic photon flux density of 1500 µmol m^{-2} s^{-1} and temperature of 30 °C, relative humidity 65 % and [CO_2] of 350 ppm. [1] iA values with a common lower case letter between cultivars and water conditions are not different at Tukey 5 %. [2] Values of % of control iA with a common upper case letter are not different at Tukey 5 %.

Water constraint significantly reduced values of RUE, number of leaves, average area of a single leaf, TSLA, and $\sum PAR_{int}$ but did not statistically affect SPAD or SLW.

All cultivars had same values of RUE and total number of leaves formed. Old cultivars had significantly bigger leaves than new ones and higher total leaf area than L457. L484 had higher chlorophyll content than AC and L457, and thicker leaves than IRCO and L457.

Water constraint reduced significantly less iA for L484 than AC and L457, 95.8, 62.6 and 69.8% of control, respectively (*Pvalue = 0.020**) (Figure 22). However, it affected all cultivars similarly on LA, TSLA, $\sum PAR_{int}$ and SPAD reading (Table 18). Water constraint reduced significantly less RUE values of cultivar L484 than others and reduced RUE the most for IRCO and L457 (*Pvalue = 0.00023****). Therefore, it reduced more the total number of leaves formed of cultivar AC than of L484 (*Pvalue = 0.038**), and significantly reduced SLW and iA more for cultivar AC and L457 compared to L484 (*Pvalues of 0.015* and 0.020,* respectively).*

Table 18. Greenhouse average values of control, water-limited conditions and % of control for radiation use related variables.

Water status	Cultivars	†RUE (g MJ^{-1} m^{-2})	‡Leaf #	Single leaf average area (cm^2)	‡Leaf area (cm^2)	§$\sum PAR_{int}$ (MJ)	¶SPAD	Specific leaf weight (g cm^{-2})
Control		1.13 ††a	104.2 a	115.1 a	12288 a	104.1 a	42.8	39.5
FTSW 0.4		0.70 b	51.3 b	99.8 b	5359 b	74.4 b	43.9	41.1
	AC	0.93	79.8	112.2 b	9511 a	93.7 a	41.8 b	41.3 ab
	IRCO	0.84	68.4	132.3 a	9877 a	96.0 a	43.3 ab	35.0 b
	L457	0.86	79.3	93.8 c	7730 b	80.7 b	42.2 b	37.3 b
	L484	1.04	83.5	91.3 c	8175 ab	86.6 ab	46.1 a	47.7 a
Pvalue WS		***	***	**	***	***	‡‡*ns*	*ns*
Pvalue Cultivars		*ns*	*ns*	***	**	*	**	**
Pvalue WS x Cultivars		*ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
% of control	AC	0.62 b	42.7 b	96	44.6	70.4	100.7	99.6 b
	IRCO	0.49 c	46.3 ab	81.7	38.8	70.4	98.3	100.9 ab
	L457	0.53 c	49.9 ab	91.1	45.7	71.2	104.1	92.5 b
	L484	0.73 a	57.9 a	79.4	46.5	74.1	107.1	122.0 a
Pvalue % control		***	*	*ns*	*ns*	*ns*	*ns*	*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Radiation use efficiency
‡ Formed during full water-limited conditions (35-60 days after planting)
§ sum of intercepted photoactive radiation
¶ chlorophyll content indicator
†† Honest Significant Differences; values with a common letter between cultivars or between water status (WS) are not different at Tukey 5 %.
‡‡ *ns*, non significant at the 0.05 probability level.

3.2.2. Effects of water regime on water use components

There was no significant interaction between cultivar and water status for all variables related to water use and top weight (Table 19). Water constraint significantly reduced values of WUE (instant and long term), 24 h average global plant transpiration from 35 to 60 DAP, average water transpiration per cm² of leaf in 24 h, stomatal conductance and top weight. Delta ^{13}C had a significantly bigger value for water-limited than control plants. There was no significant difference between cultivars for the average global plant transpiration in 24 h, delta ^{13}C and top weight. IRCO had a significantly higher WUE than L457. Cultivar L484 had significantly higher average water transpiration per cm² of leaf in 24 h value than old ones.

Relative activity (% of control) was the same for all cultivars for delta ^{13}C, WUE_i, stomatal conductance and top weight. L484 had the lowest reduction of transpiration (global and per leaf area (same as AC)) and WUE (same as AC and L457) of all cultivars.

Table 19. Average values of control, water-limited conditions and % of control for water use efficiency (WUE) related variables.

Water status	Cultivars	†WUE (g l^{-1})	‡Plant transpi (g $plant^{-1}$ $24h^{-1}$)	‡Leaf area transpi (g cm^{-2} 24^{-1})	§$\Delta^{13}C$	top weight (g)	¶WUE_i (µmol $mmol^{-1}$)	Stomatal conductance (mmol m^{-2} s^{-1})
Control		3.10 ††a	2498 a	0.41 a	-28.7 b	120.2 a	9.04 a	222 a
FTSW 0.4		2.88 b	1101 b	0.32 b	-28.2 a	55.3 b	7.98 b	181 b
	AC	3.03 ab	1878	0.35 b	-28.2	93.8	9.10 a	185
	IRCO	3.18 a	1772	0.30 c	-28.4	90.1	8.27 ab	194
	L457	2.73 b	1658	0.39 ab	-28.8	71.9	7.65 b	209
	L484	3.03 ab	1890	0.42 a	-28.5	95	9.01 a	216
Pvalue WS		*	***	***	**	***	**	***
Pvalue Cultivars		*	‡‡*ns*	***	*ns*	*ns*	**	*ns*
Pvalue WS x Cultivars		*Ns*	*ns*	*ns*	*ns*	*ns*	*ns*	*ns*
% of control	AC	91.6 ab	48.8 b	86.2 a	96.9	42.7	87.2	71.5
	IRCO	80.7 b	46.4 b	74.0 b	97.9	35.1	86.6	91.1
	L457	83.3 ab	48.9 b	77.8 b	99.5	36.5	88.6	78.8
	L484	96.9 a	58.0 a	88.1 a	98.7	53.2	91.0	85.2
Pvalue % control		*	***	***	*ns*	*ns*	*ns*	*ns*

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
*** Significant at the 0.001 probability level.
† Water use efficiency
‡ Measured during full water-limited conditions (35-60 days after planting)
§ Delta in isotope 13 carbon
¶ Instant water use efficiency
†† Honest Significant Differences; values with a common letter between cultivars or between water status (WS) are not different at Tukey 5 %.
‡‡ *ns*, non significant at the 0.05 probability level.

4. Discussion

Our objective was to study the effect of water deficit conditions on plant morpho-physiological traits of cotton cultivars widely cultivated in Cameroon. Using both field and greenhouse experiments, we reproduced a wide range of water deficit conditions from no deficit to intense water deficit starting from the beginning of crop cycle. Cultivar L484 is of interest in this discussion because it showed pattern of adaptation to early stress conditions and is currently cultivated in the more limiting water conditions in Cameroon (Far North region).

4.1. Water deficit impact on plant morpho-physiological traits

Average FTSW ranged from 0.39 to 0.83 (Figure 21), with similar level in the greenhouse water deficit and the field conditions of CMG C (close to 0.4). As expected, water deficit had a negative impact on almost all plant functions, both under field and controlled environments (Hsiao, 1973). Water deficit shortened the duration of crop cycle (Table 15). This was due to shorter duration from anthesis to boll opening which was reduced by 121 GDD (9 days) with water constraint. "Duration from planting to anthesis was not expected to differ between CMG since there was no major water limitation during that period. From emergence, plants reached anthesis with a maximum difference of 31 GDD (2 days), probably due to the difference of N1BF (Tables 15 and 16). In water deficit conditions, nodes appeared slower compared to the best conditions and crop cycle was globally shorter. As a result, plants developed fewer nodes on the main stem. The internode length was statistically different between CMG but with a maximum difference of 2% between each. Consequently with fewer nodes, water-limited plants were shorter. Based on the radiation use description (Figure 19), results showed that water-limited plants had fewer and smaller leaves, lower total leaf area (Tables 3 and 5) and hence intercepted less radiation compared to well-watered plants. Soil water availability did not affect leaf thickness and chlorophyll content**.** However, it reduced net photosynthesis of cotton leaves as indicated by iA (Figure 22), similar to Ackerson et al. (1977) and Chastain et al. (2014). As a result, the RUE was reduced by water-limited conditions. Therefore, with a lower RUE and smaller amount of radiation intercepted, water-limited plants produced less biomass (Tables 17-19). Papastylianou and Argyrokastritis (2014) also found a smaller total leaf area in Mediterranean deficit irrigated conditions and smaller biomass compared to optimal conditions.

Based on the water use description (Figure 19), results showed that water-limited plants globally transpired less compared to well-watered ones, as their global and leaf unit transpirations were

reduced similar to Singh et al. (2015). Overall stomatal closure and transpiration reduction in response to water deficiency have long been established (Hsiao, 1973). We also found that water-limited conditions lowered the water transpired by stomatal closure. The WUE (instant and long term) were smaller in water limited conditions compared to control probably because assimilation was more affected than transpiration. Hence, with smaller transpiration and WUE, stressed plants produced less biomass compared to control.

Our results showed that both radiation use and water use ways could explain the lower biomass produced in water deficit conditions. We found that these conditions also reduced the allocation of biomass to reproductive organs and hence cotton yield. With a lower cotton yield and a lower average lint percentage across cultivars, the water deficit conditions clearly reduced lint yield. Nord and Lynch (2009) also found that water deficits generally reduced yield, while Papastylianou and Argyrokastritis (2014) found that the lint percentage was not affected by water deficit. Ranking of cotton yield between CMG was also due to globally earlier planting dates in the best CMG compared to the second best and the last, reduced yield with delayed planting was also observed in similar conditions in Mali (Traore et al., 2014). Overall, we observed that the impact of water-limited conditions was similar in both field and greenhouse before and after anthesis.

4.2. Water limitation impact on RUE, WUE and [1]EUW of L484

Anthesis date is linked to the date of first fruiting branch apparition. We found that anthesis date was the same for all cultivars (Table 15). However cultivar L484 had a faster phyllochron than AC but it was compensated with a higher N1BF. Thus, its first fruiting branch appeared at the same time as other cultivars. In early water deficit conditions, L484 had smaller leaves but its number of leaves were not much affected (% of control) compared to the older cultivars (Table 18). Therefore L484 produced similar leaf area to the other cultivars. We considered that all cultivars had the same *k*. Consequently, L484 should have intercepted as much radiation as older cultivars, since it had produced as much biomass, and had the same RUE (Tables 18 and 19). Nonetheless, L484 had smaller leaves compared to ancient cultivars and we may have overestimated its *k* and thus the amount of radiation it had intercepted. In that case, L484 should have higher RUE compared to older ones which would be consistent with its higher values of assimilation rate observed in water deficit conditions compared to the other cultivars. Cultivar L484 showed thicker leaves than IRCO and L457 and in early water deficit conditions, maintained thicker leaves with more chlorophyll than AC; which is a characteristic of drought resistance (Jagmail Singh et al., 1990).

[1] *Effective Use of Water (Bloom, 2009) implies maximal soil moisture capture for transpiration which also involves reduced non-stomatal transpiration and minimal water loss by soil evaporation*

Therefore, L484 had higher instant net photosynthesis in drought conditions compared to the others cultivars (Figure 4). This probably explains why water deficit conditions did not affect much RUE of cultivar L484 compared to the other ones. The range of RUE values obtained in this paper was consistent with ones observed for conventional cotton in Australia (0.5-1.2 g/MJ/m^2) (Brodrick et al., 2013).

Cultivar L484 had higher average water transpiration per cm^2 of leaf in 24 h compared to ancient cultivars, probably due to a thinner boundary layer as a result of less hairy leaves than AC (Table 16) and higher transpiration maintenance than IRCO. Nonetheless, L484 had the same plant level water use and produced same amount of biomass as the other cultivars. Consequently, L484 had the same WUE as the older cultivars but had higher WUE_i than L457. This was due to higher assimilation rate, and similar transpiration and stomatal conductance compared to L457. The WUE values observed remained below the suggested potential of 40 kg ha^{-1} mm^{-1} (Zhang et al., 2014).

In water-limited conditions, cultivar L484 showed a relatively higher rate of development (Table 15), transpiration per leaf unit area and photosynthesis activity which is likely to decrease soil evaporation and non-stomatal use of water. Thus, we conclude that L484 may have a higher EUW (Blum, 2009) compared to other cultivars.

Cultivar L484 seemed to show some adaptation traits to early water constraint compared to other cultivars. It seemed to be better adapted to the conditions of Far North region in Cameroon, characterized by short rainy season, and insufficient rains at the beginning of the season leading to late planting (Sultan et al., 2010). Cultivar L484 maintained a high level of transpiration and photosynthesis in early water constraint conditions following a strategy of *growth maintenance*. Breeding for cultivars with same the anthesis date but with higher N1BF leads to a faster development rate (phyllochron) and therefore, shorter post anthesis cycle (Tables 15 and 16). This allows L484 to end its full crop cycle before the end of the rainy season. Furthermore, climate change predictions indicate that the rainy seasons are more likely to be variable in terms of length (Vrieling et al., 2013). The cotton breeding program in Cameroon succeeded in providing a cultivar (L484) with a better adaptation to early water constraint conditions due to a higher maintenance of physiological functions and faster development, but neither with a better potential yield in good conditions nor in case of end of season drought.

4.3. Limitation of the study and perspectives

We observed that L484 had a greater WUE maintenance in greenhouse water-limited conditions unlike IRCO. However, for L484, WUE maintenance had no impact on yield or biomass in the worst field conditions. This was probably because WUE can be associated with either high or low productivity (Saranga et al., 2004). Our results showed that despite the advances in cotton breeding in Cameroon, there was no significant increase in terms of biomass, harvest index and cotton yield in good conditions (yield potential) or in late water constraint conditions (Tables 17 and 19). The greenhouse experiment was not carried out until harvest. However, timing of stress event is critical for cotton yield (Snowden et al., 2014). Such an early and high level of water-limited conditions would have probably led to very little yield. Nonetheless, cultivar L484 showed adaptation strategies to early water deficit and could have led to higher yields compared to other cultivars in case of early water deficit found in the field. Unfortunately, no such conditions were experienced *in campo*. In this study, we used the most different cultivars released by breeding in Cameroon in terms of development and morphology (chapter 1, and transition between chapter 1 and 2) and it happened that these cultivars showed very few significant differences in field late drought conditions. In order to better understand drought adaptation strategies in cotton, we recommend including additional cultivars from completely different ecotypes or those genetically modified (GMO) with drought adaptation traits if acceptable. Under water constraint, such GMO were shown to display delayed leaf senescence with more root and shoot biomass, reduced boll abscission, higher chlorophyll content and photosynthetic in comparison to wild-type (Kuppu et al., 2013). Use of GMO cotton cultivars was not an option in our case since there was no legal agreement with Cameroon to do such field experiments. The cotton cultivar J-13 from China (Chen et al., 2013) showing strong early water constraint adaptation should be promising for rainfed conditions of Northern Cameroon as it would allow early planting consequently leading to better yields. Finally we recommend the study of plant recovery dynamics after water constraint release. This trait is determinant to ensure that cultivars could reach the end of their full crop cycle before the end of the rainy season, even when facing several mild water limitations during the cycle.

5. Conclusion

Breeding for cotton quality in rainfed conditions often also improves drought yield adaptation. Cultivar L484 had a fast development and maintained high transpiration and photosynthetic activity when strong water limitations occurred at the beginning of the crop cycle and could be described as a cultivar with a *growth maintenance* strategy. However, cotton yield has not been improved for decades irrespective of the level of water availability. In addition, field conditions are not sufficiently discriminant to study the response of cultivar to changing climate. Crop modelling can evaluate the impact of climate change on cotton (Gérardeaux et al., 2013; Voloudakis et al., 2015) and could be a good supplement to the traditional use of experimentation in cultivar breeding and post-registration field testing (Jeuffroy et al., 2014). This will allow focusing on mechanisms which cannot be measured *in campo* and are easily represented *in silico* and related to yield in drought conditions.

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Ideotypes design by simulation

This chapter was adapted from Loison, R., Audebert, A., Debaeke, P., and Gérardeaux E. Designing African Rainfed Cotton Ideotypes by Simulation. In preparation for European Journal of Agronomy.

Abstract

Crop simulation models (CSM) dynamically estimate agricultural production as a function of weather and soil conditions, and crop management. They can be used for evaluating cultivars in actual and future tropical conditions. In Northern Cameroon, cotton (Gossypium hirsutum L.) is grown exclusively in rainfed conditions and its yield has been decreasing steadily since the 80s. Therefore our objectives were to evaluate the usefulness of CSM to identify current rainfed cotton ideotypes for two contrasted environments in northern Cameroon. Based on field observations constituting the minimum dataset, phenology, morphology, leaf area index and yield simulated by CROPGRO-Cotton were successfully calibrated and validated in our conditions. Results showed that ideotype should have earlier anthesis date, longer reproductive duration, thicker leaves with higher potential assimilation rate compare to the reference cultivar (L484). In the North region, it seemed that having bigger leaf than L484 should be favorable whereas in the Far North smaller ones are more suitable to local drought-prone conditions. We concluded that morpho-physiological traits could and should be imported into breeding programs in F5 generation where high genetic diversity still exist and plant material start to be considered as a line rather than a single plant. Consequently, we invite breeders to target cultivars with low "emergence to anthesis" to reproductive ratio, thick leaf, high chlorophyll content, and smaller leaf for the conditions with the lowest water availability and bigger ones for the conditions with best water availability.

1. Introduction

Crop simulation models (CSM) estimate agricultural production as a function of weather and soil conditions, and crop management. These models dynamically calculate both rates and state variables usually from planting to harvest. The CSM can be used as decision tools to support tactical and strategic management (Garcia-Vila and Fereres, 2012; Hammer and Muchow, 1994). They were successfully used for optimizing planting date (Kim et al., 2013; Z. Liu et al., 2013), fertilization and irrigation amounts and dates (Garcia-Vila and Fereres, 2012; Voloudakis et al., 2015), pest management (Elings et al., 1997), studying the impact of climate variability and climate change (Gérardeaux et al., 2013; He et al., 2015; Rotter et al., 2013; Xiao and Tao, 2014), quantifying environmental pollution (Basso et al., 2010), and evaluating cultivars (He et al., 2015; Xiao and Tao, 2014). Some CSM were proved successful in predicting yield for several crops in African rainfed conditions (millet in Niger (Rezaei et al., 2014), wheat in North Africa (Heng et al., 2007)) including cotton (Gérardeaux et al., 2013).

In Northern Cameroon, cotton (*Gossypium hirsutum L.)* is the first cash crop grown exclusively in rainfed conditions (Sultan et al., 2010). In these conditions, seed cotton yield is widely affected by the climate conditions and especially by the rainfalls pattern (M'Biandoun and Olina, 2006). This is especially true in the driest cotton areas (Far North region) where cotton yield is the most sensitive to rainfall variability (Sultan et al., 2010). In addition, in the Northern Cameroon, rainfalls already showed very high spatial and over time variability (M'Biandoun and Olina, 2006) and this variability is likely to increase (Sultan et al., 2010).

Despite a breeding program, seed cotton yield has been decreasing steadily since the 80s in Northern Cameroon (Naudin et al., 2010). This could result from the increasing numbers of farmers adopting unsuitable cropping practices for cotton (reducing fertilizer, cultivating infertile plots, and late planting (Cao et al., 2011)), and also from breeding targeting sub-optimal conditions but based on "defect elimination" or "selection for yield" (Donald, 1968) but not on targeted ideotypes. A crop ideotype was originally defined as a "plant model which is expected to yield a greater quantity or quality of grain, oil or other useful product when developed as a cultivar" within a defined environment (Donald, 1968). Then, it was recently defined as "a combination of morphological and/or physiological traits, or their genetic bases, optimizing crop performance to a particular biophysical environment, crop management, and end-use" (Martre et al., 2015). When resulting from simulation with CSM using morpho-physiological traits, our

definition of ideotype here was adapted from the one by Rötter et al. (2015), defined as "a set of crop or cultivar parameters that define [optimal] growth and development of a crop with the given environmental conditions." Decreased yields along with higher variability are expected in tropical regions (Challinor et al., 2014) and uncertainties of climate change projections are challenging plant breeders and crop scientists (Semenov et al., 2014). In order to support them in their quest for new cultivars in an uncertain future, changing model genetic parameters from existing ranges and optimizing them for yield in response to changing climate or to existing environmental conditions, was reviewed to be successful in the design of ideotypes showing the best yield (Rötter et al., 2015). Consequently, the usefulness of CSM combining physiology and genetic parameters should be guaranteed in the design of rainfed cotton ideotype in the low fertility soils (Mahop and Van Ranst, 1997) of Northern Cameroon cotton production area of today but also in the context of climate change. To our knowledge, the use and evaluation of CSM for rainfed cotton ideotype designing has never been studied.

Therefore our objectives were to:

i/ evaluate two existing rainfed cotton cultivars in a generated climatic series of 99 years and in two locations in Cameroon.

ii/ identify current rainfed cotton ideotypes for both locations.

2. Material and methods

2.1. Overview of adopted methodology for ideotype design by simulation

An illustration of the procedure used by this study for ideotyping with CSM is given in Figure 23.

A minimum dataset is needed in order to be able to use CSM inputs of soil characteristics, climate data, and agronomic measurements. Then, genetic parameters were fitted to reduce gaps between simulation and observation for phenology, morphology, biomass, and yield variables. Calibration was considered good enough when simulation represented observed crop phenology, development, morphology, biomass, and also yield below a RMSE (root mean square error) threshold. In this study, we considered that calibration was successful when anthesis, 1st boll opening were predicted within one week maximum from observed dates and maximum leaf area RMSE was below 0.5 and seed cotton yield RRMSE was below 40% of measured values.

Model validation consists in having a good representation of ecophysiological processes and final production with parameters calibration in independent conditions. Calibration and evaluation are two important steps prior to the application of CSM (Yang et al., 2014). When the CSM cannot be calibrated, it is probably because the model structure is not suitable to answer to the question asked. When the model was properly calibrated but cannot be validated, it reveals that some important processes were omitted. In the latter, one should go back to model development and go through another round of calibration then validation. Once the CSM is validated or evaluated as suitable for study purposes, we can proceed to its application. For that, it is necessary to prepare a virtual experience plan with the factors of interest.

In this study, two cultivars widely grown on more than 100 000 ha in Cameroon were compared in different environments. Cultivar AC was released in Cameroon in 1950 and L484 in 2008. DSSAT CROPGRO-Cotton was already successfully calibrated and validated for Cameroonian conditions (Gérardeaux et al., 2013). We proceeded to a new calibration for our cultivars L484 and AC, followed by a validation in independent cropping conditions according to the methodology described in Gérardeaux et al. (2013). Then, we generated a simulated climatic series based on a real NASA (National Aeronautics and Space Administration) data, and designed several virtual cultivars (VC) to be evaluated as candidate ideotypes for Cameroonian rainfed cotton area.

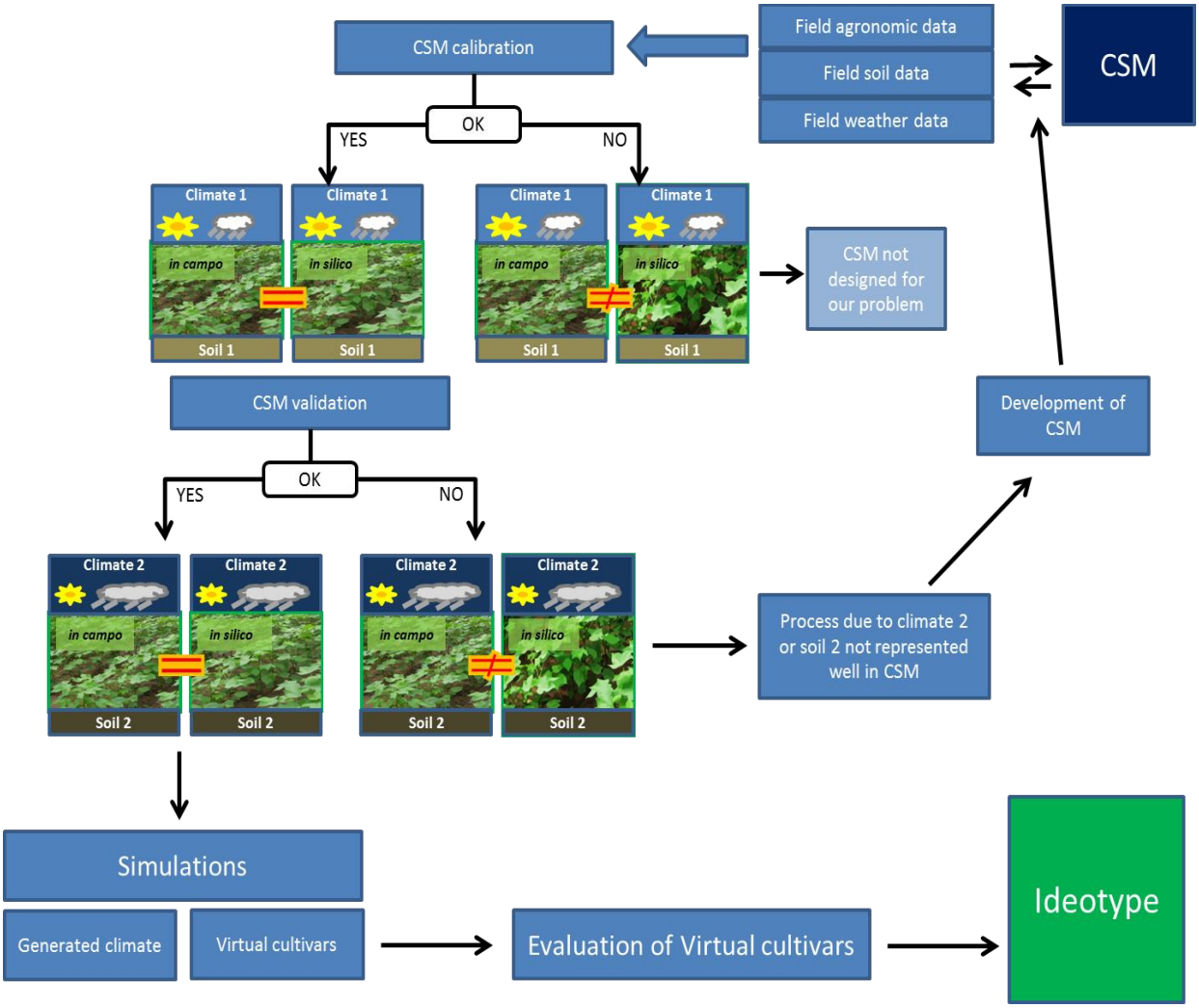

Figure 23. Procedure for ideotype design by crop simulation model (CSM).

2.2. Description of the crop simulation model DSSAT CROPGRO-Cotton

The CSM CROPGRO is composed of several modules: soil, weather, soil-plant-atmosphere, management, and crop (Jones et al., 2003). As described by Pathak et al. (2007), the soil module includes soil water, soil temperature, soil carbon, and nitrogen dynamics in a one-dimensional vertical layers profile. The weather module provides measured or generates daily weather (at least minimum and maximum air temperatures, solar radiation, and precipitation). The soil-plant-atmosphere module computes daily soil evaporation and plant transpiration. The management module determines timing and characteristics of management practices on the system (planting, tillage, harvesting, inorganic fertilization, irrigation, and application of crop residues or organic materials). Finally, the crop module predicts the growth, development and yield of various crops. Each crop is described with its own set of genetic parameters. There are three sets of genetic parameters that account for differences in development, growth, and yield between species, ecotypes, and cultivars (Boote et al., 2003). We invite the reader to refer to Pathak et al. (2007) for a more comprehensive description of this CSM and Thorp et al. (2014) for detailed concepts used in DSSAT CROPGRO-Cotton. DSSAT CROPGRO-Cotton has already been used in African rainfed conditions on cotton crop (Gérardeaux et al., 2013) and contains a wide range of genetic parameters which make it suitable for ideotype targeting by simulation.

2.3. Field description and agronomic data collected

Field experiments on research stations in Cameroon were located in Sanguéré (9.25 N, 13.47 E) and Kodeck (10.65 N, 14.41 E) in 2012, and in Sanguéré and Soukoundou (9.84 N, 13.87 E) in 2013. Difference between cropping conditions resulted from different locations (onset of rainy season, soil properties, and precipitation pattern and amount), planting dates and fertilization levels (associated to planting dates). In 2012, planting dates were 14 June, 27 June, and 11 July in Sanguéré, and 6 July and 19 July in Kodeck. In 2013, they were 8 July and 22 July in Sanguéré, and 4 July and 18 July in Soukoundou. Soil texture was loamy sand in Sanguéré, loam in Kodeck, and sandy clay loam in Soukoundou. Total available water storage capacity was 206 mm, 84 mm, and 150 mm, respectively. Plant density was 31250 plants ha^{-1} with row width of 0.8 m. Fertilization was 200 kg ha^{-1} of composite fertilizer (NPKSB 22-10-15-5-1%) at early crop stage for early planting in all locations and years. It was only 150 kg ha^{-1} for mid-late planting in Sanguéré 2012. For all other conditions, only 100 kg ha^{-1} was applied at early crop stage. At ridging, 50 kg ha^{-1} of urea (46 % N)

was applied for all cropping conditions except in Kodeck and in the late planting in Sanguéré 2012. Insecticides were used to control the bollworm (*Helicoverpa armigera*) and the aphid (*Aphis gossypii*), and manual weeding was performed whenever needed.

Phenology, morphology, leaf area index, biomass, yield components and seed cotton yield were measured as described in material and methods of chapters 1 and 2.

2.4. Weather conditions

In 2012 and 2013, synoptic weather stations located within 10 km from the field recorded temperatures, solar radiation, dew point temperature, and wind speed. Precipitation was measured daily on the fields.

In order to generate extra years of climate for Sanguéré and Kodeck, we used eighteen years of measured weather data provided by the NASA for each location. Monthly average of these values is presented in Figure 24. Sanguéré has a longer rainy season with higher total rainfall (1041 mm) compared to Kodeck (855 mm). Monthly average temperatures were similar in the two locations, minimum ranging from 19.9 to 25.4 °C in Sanguéré and 19.4 to 26.5 °C in Kodeck and maximum 27.9 to 38.7 °C in Sanguéré and 28.8 to 39.8 °C in Kodeck. The GPS coordinates of the two stations studied were Sanguéré (9.246 N, 13.471 E) and Kodeck (10.652 N, 14.410 E). In Sanguéré and in Kodeck, 99 years of weather conditions were generated from the NASA weather data using stochastic weather generator WGEN (Richardson, 1985, 1981).

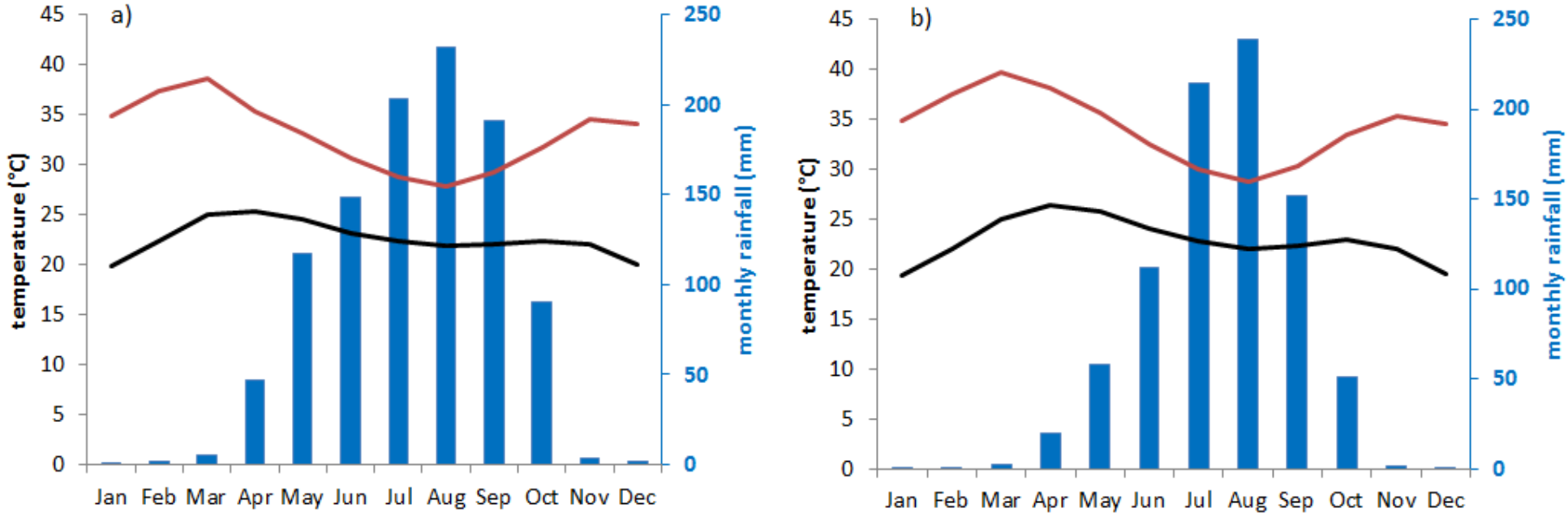

Figure 24. Monthly average maximum (red) and minimum (black) temperatures and total rainfall (blue) for Sanguéré (a) and Kodeck (b) in Cameroon from 1997 to 2014.

Weather data measured by the NASA available online (http://power.larc.nasa.gov/cgi-bin/cgiwrap/solar/agro.cgi?email=agroclim@larc.nasa.gov); Sanguéré (9.246 N, 13.471 E) and Kodeck (10.652 N, 14.410 E).

2.5. Seasonal analysis

For each of the 99 years simulated in each location, planting was simulated from 1st of June to end of July as soon as soil moisture reached 60 % for the top 30 cm. Plant density considered was 31250 plants ha^{-1} with row width of 0.8 m. Application of 44 kg ha^{-1} of N in a complete fertilizer at 10 days after planting (DAP) and 50 kg ha^{-1} of urea (46% of N) at 45 DAP. Soils used were the ones used for the calibration: Sanguéré 2012 and Kodeck 2012. Cotton was harvested on 10 December of each year. Finally the CO_2 air concentration was fixed at 380 vpm.

2.6. Generation of virtual cultivars

In order to generate virtual cultivars (VC) with different phenotypes, we modified the values of genetic parameters which govern the main plant functions: (i) phenology: phase duration before and after anthesis, (ii) photosynthesis: maximum assimilation rate and specific leaf area, and (iii) light interception: maximum size of a fully expanded leaf. Forty-two VC were compared to the most recent cultivar calibrated (L484) in DSSAT CROPGRO-Cotton seasonal simulations over the 99 years of climate generated in each location. In order to create these cultivars, five (cultivar) genetic traits were either reduced or increased by 20% from the calibrated L484 reference. These five traits were the duration from emergence to flowering (EM-FL, thermal days) and from 1st seed to 1st open boll (SD-PM, thermal days), the maximum leaf photosynthesis rate at 30°C, 350 vpm CO2 and under high light conditions (LFMAX, mg [CO_2] m^{-2} s^{-1}), the specific leaf area under standard growth conditions (SLAVR, cm^2 g^{-1}), and the maximum size of full leaf (SIZLF, cm^2). The VC L484_02 to L484_11 differed from the reference by only one trait (Table 20) while the VC L484_12 to L484_43 combined the five traits modifications at the same time.

Table 20. List of cultivars compared in DSSAT CROPGRO-Cotton simulations.

Cultivar	EM-FL	SD-PM	LFMAX	SLAVR	SIZLF
L484 REF					
L484_02	-				
L484_03	+				
L484_04		-			
L484_05		+			
L484_06			-		
L484_07			+		
L484_08				-	
L484_09				+	
L484_10					-
L484_11					+
L484_12	-	-	-	-	-
L484_13	-	-	-	-	+
L484_14	-	-	-	+	-
L484_15	-	-	-	+	+
L484_16	-	-	+	-	-
L484_17	-	-	+	-	+
L484_18	-	-	+	+	-
L484_19	-	-	+	+	+
L484_20	-	+	-	-	-
L484_21	-	+	-	-	+
L484_22	-	+	-	+	-
L484_23	-	+	-	+	+
L484_24	-	+	+	-	-
L484_25	-	+	+	-	+
L484_26	-	+	+	+	-
L484_27	-	+	+	+	+
L484_28	+	-	-	-	-
L484_29	+	-	-	-	+
L484_30	+	-	-	+	-
L484_31	+	-	-	+	+
L484_32	+	-	+	-	-
L484_33	+	-	+	-	+
L484_34	+	-	+	+	-
L484_35	+	-	+	+	+
L484_36	+	+	-	-	-
L484_37	+	+	-	-	+
L484_38	+	+	-	+	-
L484_39	+	+	-	+	+
L484_40	+	+	+	-	-
L484_41	+	+	+	-	+
L484_42	+	+	+	+	-
L484_43	+	+	+	+	+

Cultivars were L484 calibrated (L484 REF) and 42 other virtual cultivars with 20% reduction (-) or increase (+) from the reference value for emergence to flowering duration (EM-FL), 1st seed to 1st open boll (SD-PM), carbon dioxide assimilation rate (LFMAX), specific leaf area (SLAVR), and maximum area of a single leaf (SIZLF). When cell is empty there was no modification of the trait for the corresponding cultivar.

3. Results

3.1. Observed leaf area index of the two cultivars across all cropping conditions

Across all cropping conditions in Sanguéré, Kodeck and Soukoundou, cultivar L484 tended to have smaller LAI compared to AC as demonstrated by paired t-tests. They showed that AC and L484 had same LAI for values below 0.8 but for LAI values greater than 0.8, AC had greater LAI compared to L484 (*Pvalue = 0.049 **) once outliers were removed with local outlier factor algorithm from R package {DMwR} (Torgo, 2010); 4 outliners identified with *k*=5 neighbors and LOF score above 1.5. On the Figure 25, most points were below the 1:1 line for higher values of LAI of AC than 0.8 (Figure 25).

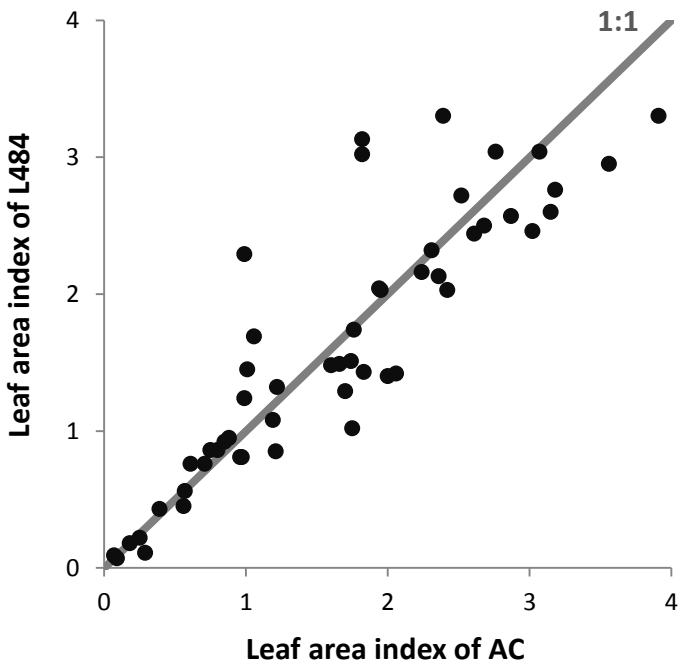

Figure 25. Measured leaf area index (LAI) of cultivar L484 as a function of AC LAI.
For higher values than 0.8, cultivar L484 tends to have smaller LAI compared to AC as most points are below the 1:1 line.

3.2. Calibration and validation of DSSAT CROPGRO-Cotton for AC and L484 in Cameroon

3.2.1. Genetic coefficients of calibrated cultivars

In one hand, calibrated cultivars AC and L484 shared common genetic coefficients. Both were not photosensitive (Critical short day length (CSDL) of 23 h), they had the same phenologic phase duration EM-FL, FL-SH (1st flower to 1st pod), FL-SD (1st flower to 1st seed), SD-PM and FL-LF (1st flower to end of leaf expansion) of 49.27, 4, 16.23, 18.05, and 76.17 thermal days, respectively. Both cultivars had the same threshing ratio of 70% (THRSH), maximum biomass allocation to reproductive organ of 80% (XFRT), and time required for cultivar to reach pod load under optimal conditions of 10 thermal days (PODUR) and seed filling duration of 15.32 thermal days (SFDUR).

On the other hand, some other genetic coefficients were specific to each cultivar (Table 21). In order to account for higher ginning out-turn of L484 compared to AC, smaller values of seed protein and lipid contents were considered in L484 seeds compared to AC (SDPRO and SDLIP). Cultivar L484 had smaller (SIZLF), thicker (SLAVR) and more photosynthetic (LFMAX) leaves compared to AC. In order to represent better the number of nodes, the phyllochron was slightly faster for AC than L484 (TRIFL).

Finally, cultivar L484 showed a higher resilience in water limited conditions, with greater leaf area transpiration and photosynthesis maintenances in drought conditions compared to AC (data from Chapter 2, not shown). Consequently, cultivar L484 was attributed a lower threshold value of potential root water uptake to potential evapotranspiration for leaf expansion (RWUP1). Its higher transpiration maintenance compared to AC, probably due to enhanced access to soil water despite same root system length, was represented by increased uptake per unit root length (RWUMX) and by smaller threshold value of potential root water uptake to potential evapotranspiration for photosynthesis and allocation to growth organs compared to AC (XSWFAC).

Table 21. Values of genetic coefficients of cotton cultivars L484 and AC calibrated in DSSAT CROPGRO-Cotton for Northern Cameroon conditions.

Coefficients	L484	AC
Cultivar		
LFMAX	1.866	1.675
SLAVR	267.6	292.7
SIZLF	132.9	200.0
SDPRO	0.180	0.183
SDLIP	0.176	0.179
Ecotype		
TRIFL	0.30	0.35
Species		
RWUEP1	1.2	1.5
RWUMX	0.08	0.04
XSWFAC	0.7	1.0

3.2.2. Comparison of observed and simulated values

Phenology of the two cultivars was properly calibrated and validated with a RMSE inferior to 3.4 days for the anthesis and to 6 days for the crop physiological maturity (Table 22). The emergence day is not perfectly predicted but it has a small impact on the following phases since it delayed the cycle only for about 1 day. Globally, the model underestimated the existing differences in phenology.

Likewise, number of nodes on the main stem, LAI max, and canopy height were properly calibrated and validated with RMSE peaking at 3.8 nodes, 0.8, 20 cm, respectively. Node number on main stem and LAI max existing variability were slightly overestimated by the model. The range of canopy height was pretty well represented.

Finally, top weight, harvest index, and seed cotton yield were averagely well calibrated and validated with RMSE peaking at 1783 kg ha^{-1}, 10%, 505 kg ha^{-1}, respectively. Threshing percentage showed a calibration RMSE of 13.4%. Existing variability was pretty well simulated for top weight, harvest index and seed cotton yield. However, it was simulated two times higher than existing for the threshing percentage.

Table 22. CROPGRO-Cotton calibration and validation across cultivars (AC and L484) in Cameroon.
Field experiments used for the calibration were Sanguéré early planting date in 2012, Sanguéré early and late planting dates in 2013, and Kodeck late planting date in 2012. Field experiments used for the validation were Sanguéré mid and late planting dates in 2012, Kodeck early planting date in 2012, and Soukoundou early and late planting dates in 2013.

Variable Name	CALIBRATION						VALIDATION					
	Mean		#SD		¶RMSE	††RRMSE	Mean		SD		RMSE	RRMSE
	†Obs	‡Sim	Obs	Sim		(%)	Obs	Sim	Obs	Sim		(%)
Phenology												
Emergence [‡‡DAP]	5.4	6.8	1.1	0.5	1.6	30.1	6	6.4	1.2	0.5	1.3	22.4
Anthesis [DAP]	66.1	66.5	1.6	0.9	2.3	3.4	64.1	66.8	2.8	0.8	3.4	5.3
Maturity [DAP]	109.9	110	7.6	1.3	6	5.5	108.2	110.8	4.2	0.4	4.6	4.3
Morphology												
Node number	22.9	25.1	3.3	3.7	3.8	16.7	22.3	23.5	1.6	2.4	3.1	13.9
##LAI maximum	3.1	3.1	0.5	0.8	0.3	8.6	2.9	2.9	0.2	0.7	0.8	28
Canopy height [m]	1	1.2	0.2	0.2	0.2	21.3	1.1	1.1	0.1	0.1	0.2	17.2
Biomass & Yield												
Tops wt [kg ha^{-1}]	3740	3968	2263	1489	1763	47.1	4751	4155	776	1268	1282	27
Harvest index [%]	0.27	0.35	0.13	0.12	0.08	28.9	0.35	0.36	0.09	0.1	0.1	24.3
Seed cotton yield [kg ha^{-1}]	1371	1535	1074	846	505	36.9	1658	1488	483	609	426	25.7
Threshing [%]	67.8	64.1	6.2	12.7	13.4	19.7	-	-	-	-	-	-

†Obs: observed values; ‡Sim: simulated by CROPGRO-Cotton; #SD: standard deviation. ¶RMSE: root mean square error; ††RRMSE: relative root mean square error; ‡‡DAP: days after planting; ##LAI: leaf area index.

3.2.3. *Repeated measures of leaf area index*

The LAI at any time was pretty well represented with a maximal RMSE of 0.57 (Figure 26). The model represented well the LAI for most of the crop cycle until physiological maturity (Figure 27). After physiological maturity, values of LAI were overestimated.

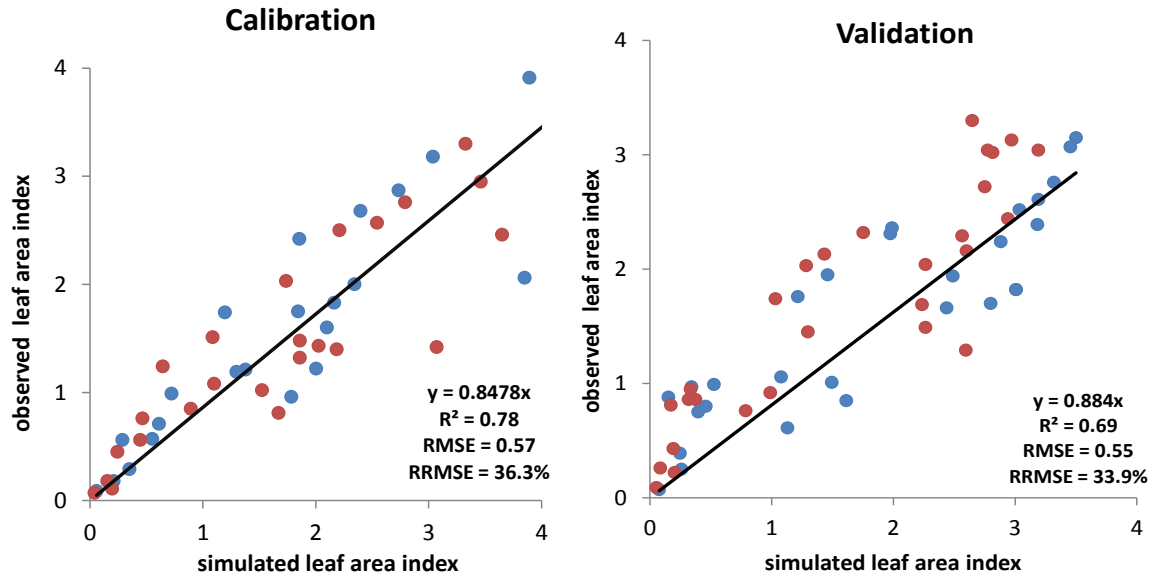

Figure 26. Calibration and validation of repeated leaf area index measured all along the cotton cycle in Cameroon.

Leaf area index was slightly overestimated and root mean square errors (RMSE) were 0.57 for calibration and 0.55 for validation. Red dots stand for cultivar L484 and blue dots for cultivar AC.

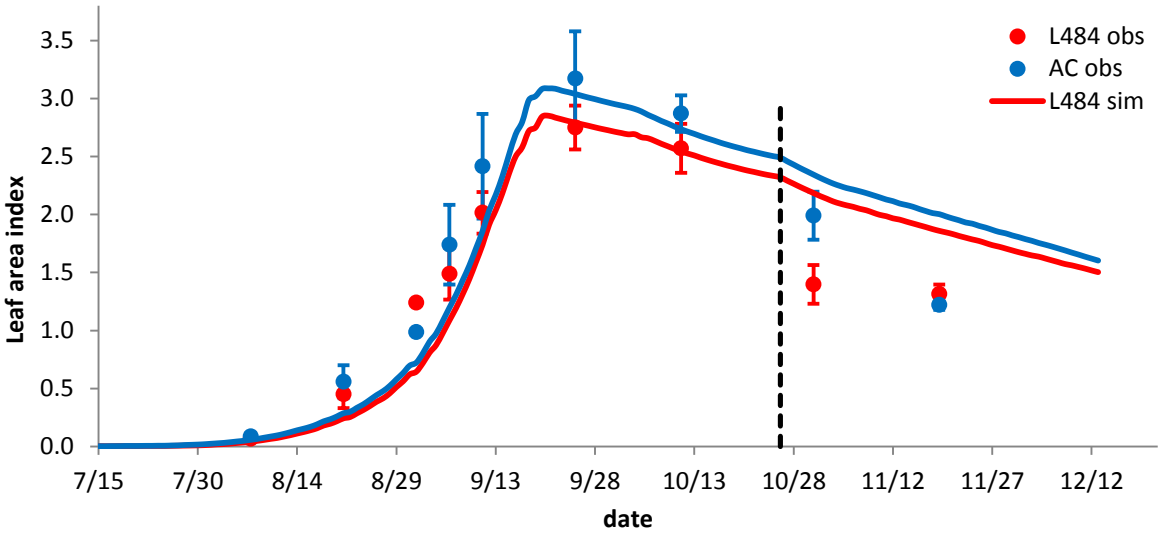

Figure 27. Calibration of leaf area index for cultivars L484 and AC in eraly planting of Sanguéré 2013.

Lines represent simulation values with DSSAT CROPGRO-Cotton. Dots represent observed values with standard errors. The dashed vertical black line correspond to the physiological maturity (1st open boll) simulated on the 26 October 2013 for both cultivars.

The model was properly calibrated; we could reasonably compare our cultivars in the 99 years of climate generated in Sanguéré and in Kodeck from past climatic series.

3.2.4. Evaluation of AC and L484 in Sanguéré and Kodeck over 99 years of generated climatic data

Cultivar AC always showed higher LAI than L484 in Sanguéré (Figure 28). In Kodeck, it was simulated the same way except for the smaller values observed (in water stress conditions) where L484 had the same or slightly higher LAI compared to AC. In Kodeck, AC and L484 had the same yield (Figure 29). On average, better yield potentials were simulated for cultivar L484 compared to AC both for the 75% higher yields in Sanguéré and the 15% higher yields in Kodeck. In addition, it seems that cultivar L484 better withstood poor conditions compared to AC. Indeed, in the first 66% lower yields in Kodeck and 15% in Sanguéré, simulated yield were higher for L484 compared to AC. In Sanguéré, for the best yields (upper 2/3), L484 had higher potential than AC. However, yield differences between these two cultivars were always smaller than the RMSE of yield (505 kg ha^{-1}) and these two cultivars yielded the same quantity of seed cotton. Since no real yield improvement was found between the ancient cultivar (AC) and recent one (L484), we will now evaluate the potential of VC for yield improvement in African rainfed cotton conditions.

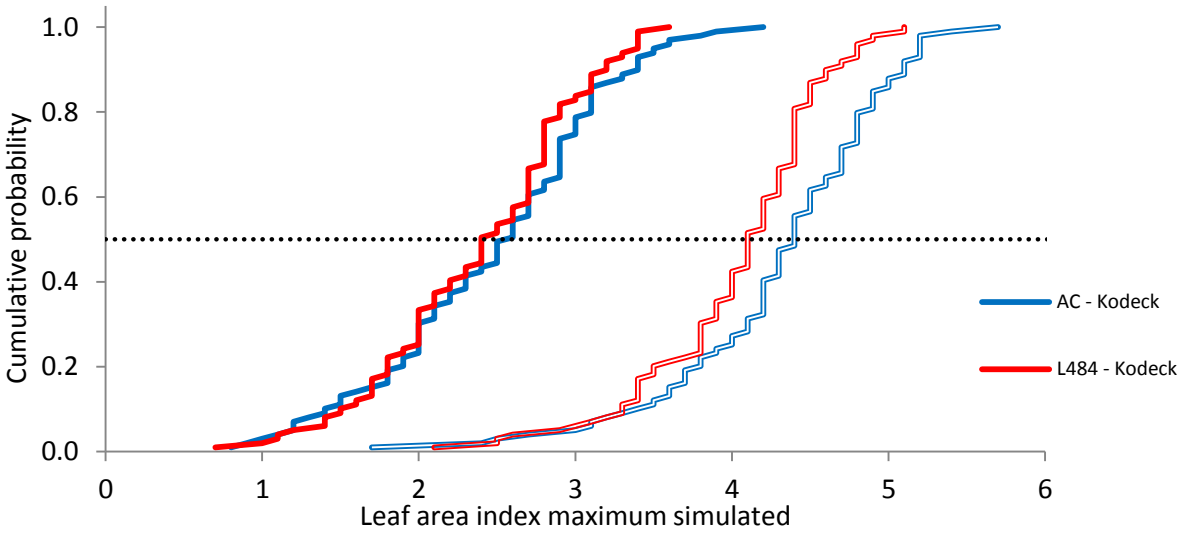

Figure 28. Leaf area index simulated by DSSAT CROPGRO-Cotton for cultivars AC and L484 in Kodeck and Sanguéré.

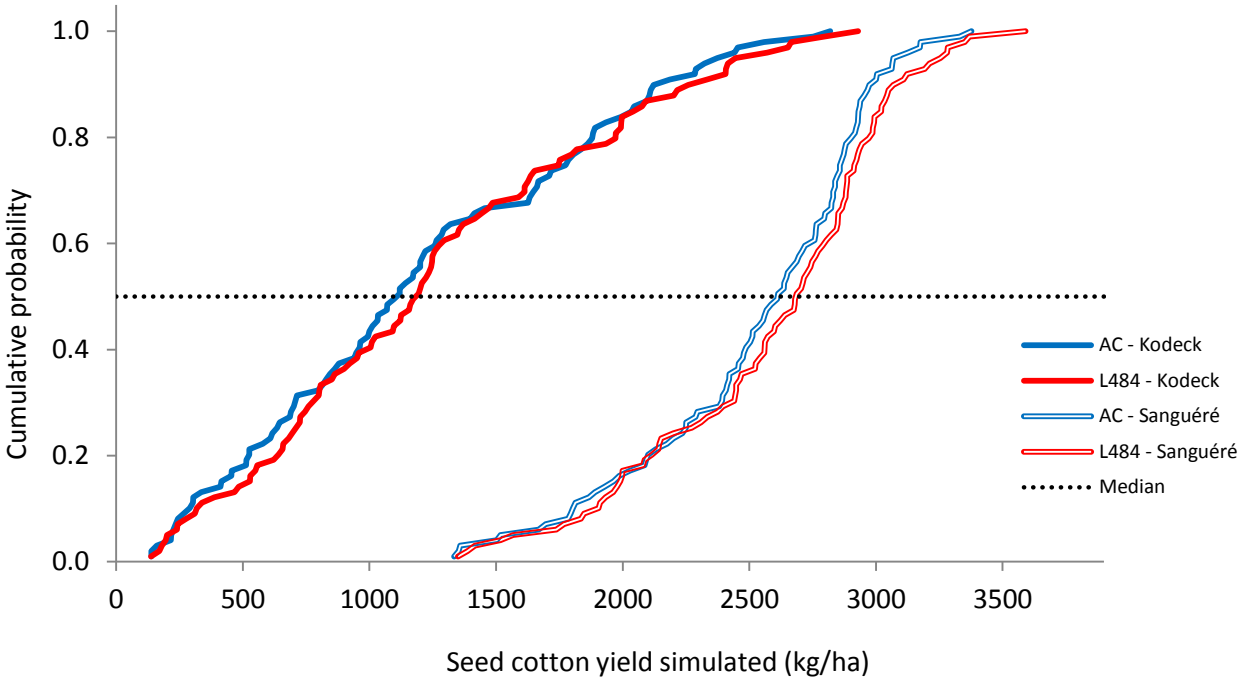

Figure 29. Seed cotton yield (kg ha-1) simulated by DSSAT CROPGRO-Cotton for cultivars AC and L484 in Kodeck and Sanguéré.

3.2.5. Simulation in two contrasting environments with virtual cultivars

In Kodeck, the model simulated seed cotton yield values of 620, 1060 and 1603 kg ha^{-1} corresponding to the centiles 25%, 50%, and 75% across all VC and years (Figure 30). The same thresholds of simulated seed cotton yield were used for Sanguéré. In Sanguéré, there was an additional threshold for greater simulated yield than 2000 kg ha^{-1} (Figure 31).

When studying the impact of each trait separately, we found that a reduction of EM-FL, an increase of SD-PM and of LFMAX would lead to increased yield in both locations. A reduction of SLAVR in Sanguéré and Kodeck (except for highest yield) led to higher yield. Finally, in Kodeck, both increase and reduction of SIZLF led to decreased yield. Reduction of SIZLF in Kodeck led to similar production in the worst conditions but to decreased yield in best conditions while increase of SIZLF was unfavorable in bad conditions and slightly better in good conditions. In Sanguéré, yield increased with leaf size.

When averaging over the 99 years L484_24 was the best VC in Kodeck and L484_25 was the best VC in Sanguéré. A comparison of these two VC and the cultivar L484 with actual weather measured in 2012 should be performed as a validation of the potential usefulness of these VC.

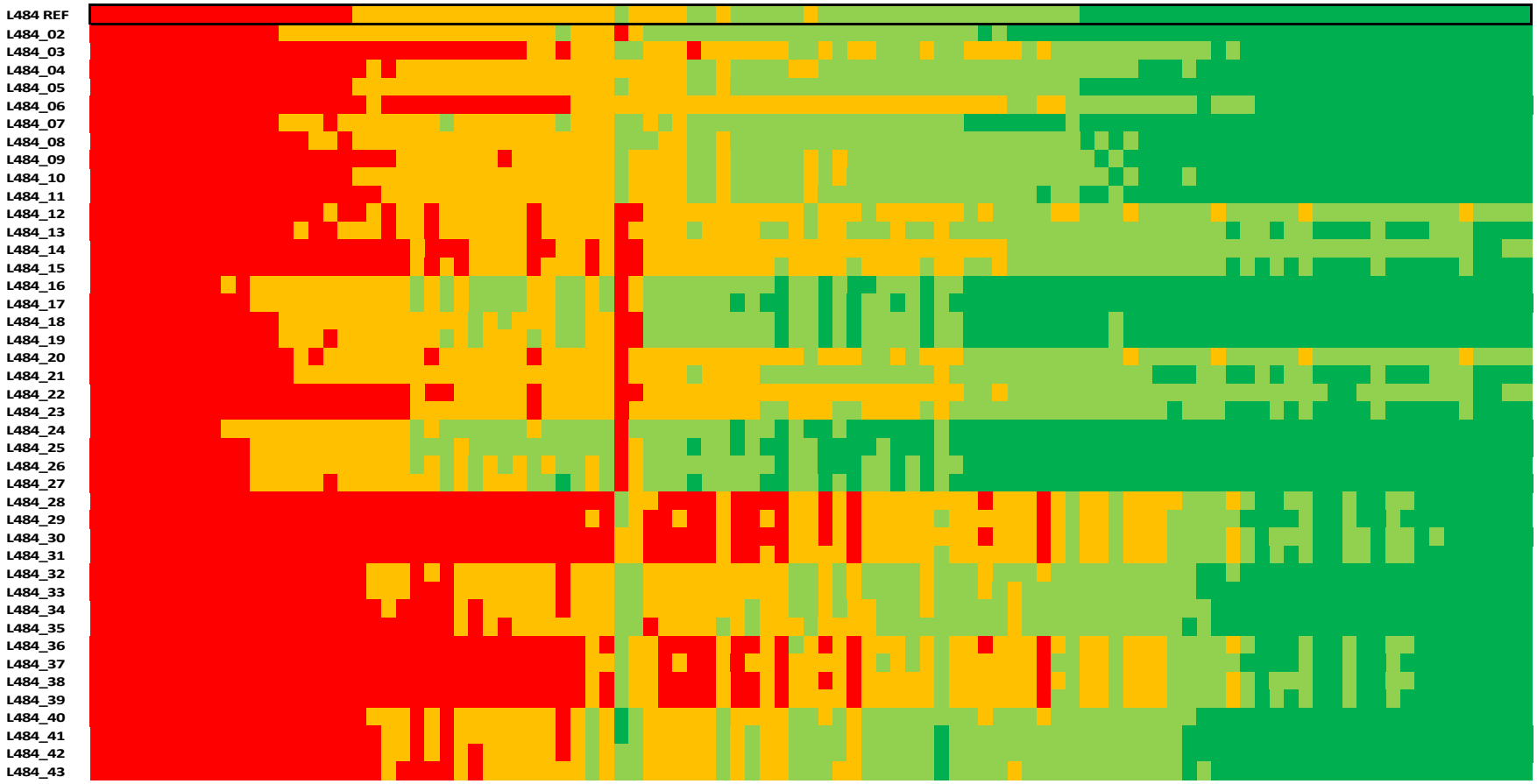

Figure 30. Simulated seed cotton yield of L484 and virtual cultivars, over 99 year of climate generated by WGEN, ranked from the worst (left) to the best potential (right) in the cropping conditions of Kodeck.

Red cells correspond to simulated yield less than 620 kg ha^{-1} (centiles 0 to 25%), orange from 620 to 1060kg ha^{-1} (centiles 25 to 50%), light green from 1060 to 1603 kg ha^{-1} (centiles 50 to 75%), and dark green above 1603 kg ha-1 (centiles 75 to 100%).

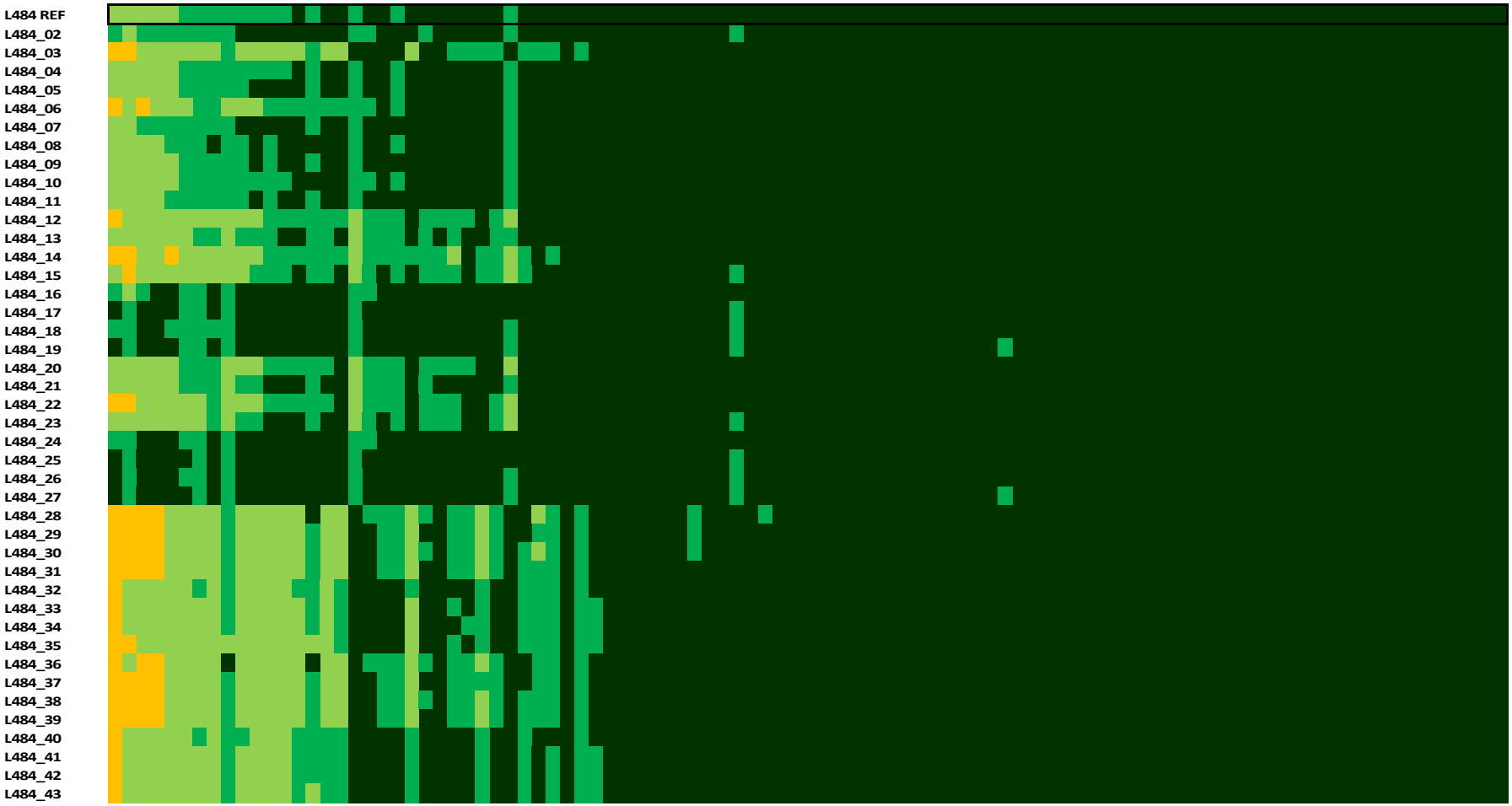

Figure 31. Simulated seed cotton yield of L484 and virtual cultivars, over 99 year of climate generated by WGEN, ranked from the worst (left) to the best potential (right) in the cropping conditions of Sanguéré.

Orange cells correspond to simulated yield between 620-1060kg ha^{-1}, light green 1060-1603 kg ha^{-1}, dark green 1603-2000 kg ha^{-1}, and super dark green > 2000 kg ha^{-1}.

3.2.6. Evaluation of virtual cultivars in field conditions of Cameroon observed in 2012

The VC L484_24 and L484_25 were compared to reference L484 in the actual field conditions of Sanguéré and Kodeck measured in 2012. The model represented some interactions between cultivars (L484 and VC) and cropping conditions on seed cotton yield (Figure 32). In Sanguéré, L484 performed the best whereas in Kodeck it was the two VC. The VC L484_24 and L484_25 performed about the same both in the best conditions found and in the worst (M1). In intermediary conditions, L484_25 looks better compared to L484_24. The VC always showed smaller LAI throughout the growing season compared to cultivar L484 (data not shown).

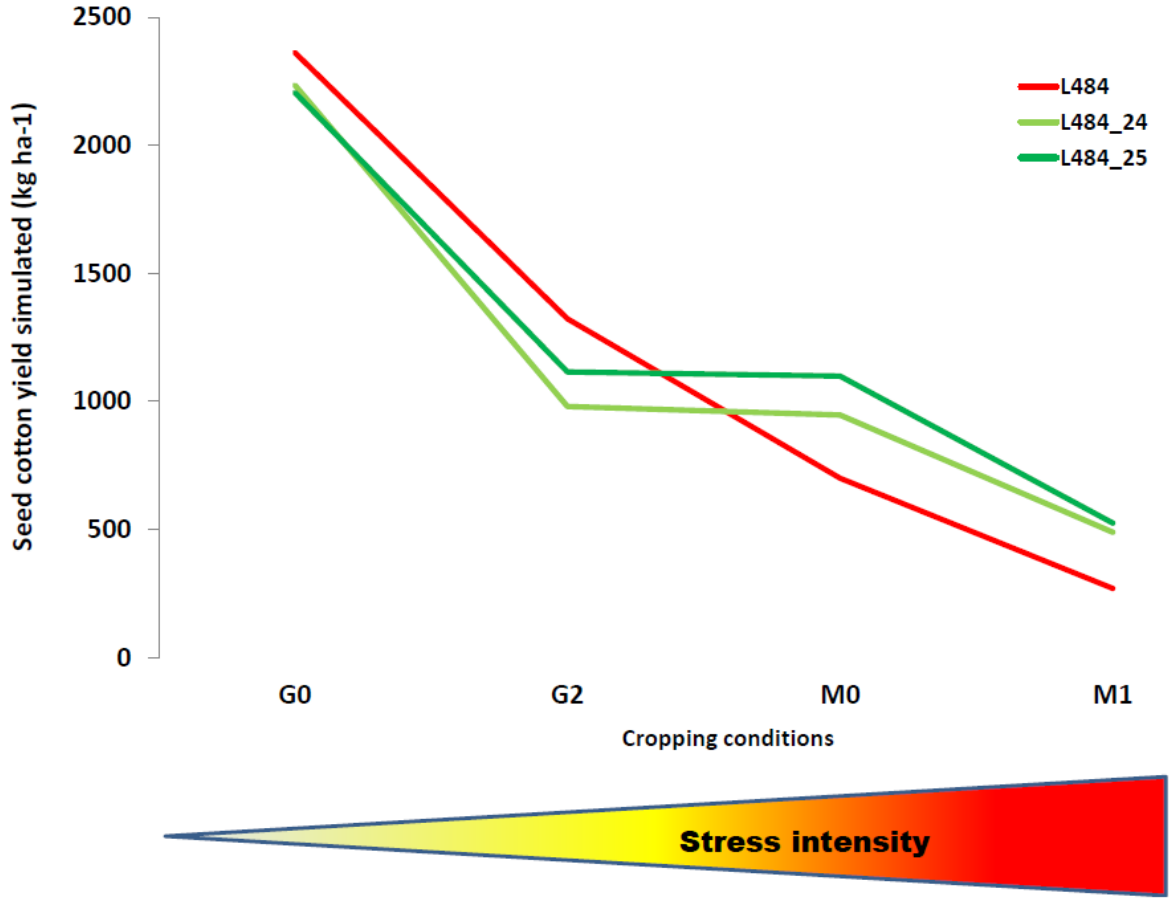

Figure 32. Simulated seed cotton yield of cultivar L484 and virtual cultivars L484-24 and L484 in field cropping conditions of Kodeck 2012 (M0, M1) and Sanguéré 2012 (G0, G2).

4. Discussion

4.1. CROPGRO calibration and validation

Our dataset availability and its quality for model calibration and validation were considered intermediate to high according to the quality standards (Grassini et al., 2015). Calibration and validation of phenology, growth, and yield were considered sufficient as confirmed by small RRMSE values (Table 22). The high value observed for top weight RRMSE (47.1 %) was due to overestimation in the most extreme drought conditions (M1, data not shown). The RMSE and RRMSE of model validation were often smaller than the ones for calibration; this was probably due to the wider range of conditions from the best field conditions to highly stress for the model calibration compared to the ones used for the model validation. The overall smaller LAI of cultivar L484 compared to AC observed in the field (Figure 25) was well represented by the model until the physiological maturity (Figures 27 and 29). The genetic parameters for both cultivars (Table 21) were representative of cultivars traits observed in previous studies with smaller and thicker leaves for L484 and higher resilience in drought conditions compared to AC (data not shown). Similar level of RMSE was found in the literature for cotton phase duration with CSM SUCROS-Cotton (Zhang et al., 2008), LAI maximum and yield using CSM DSSAT CROPGRO-Cotton (Ortiz et al., 2009) and CSM EPIC (Ko et al., 2009). We considered that DSSAT CROPGRO-Cotton was properly calibrated and validated for our conditions and was suitable for further use.

The simulations did not represent differences in yield between cultivars AC and L484 as simulated differences were always smaller to the seed cotton yield RMSE (Figure 29). In order to get higher yields in African rainfed cropping conditions, new cultivars which represent a real breaking point with existing ones are needed and virtual cultivars will be a proxy for them.

4.2. Designing ideotypes with simulation

Forty-two virtual cultivars (VC) were compared to the reference cultivar L484 in 99 generated climates for Kodeck and for Sanguéré (Figure 30 and 31). Both in the North (Sanguéré) and the Far North region (Kodeck), the best candidate ideotype had earlier anthesis date, longer reproductive duration, thicker leaves with higher potential assimilation rate compare to the reference cultivar L484. In the North region, over the 99 years, it seemed that having full size leaf bigger than L484 should be favorable whereas in the Far North it was the contrary.

Similarly, Sekloka et al. (2008) found that early flowering onset was a criteria for cotton ideotype in Sub Saharan Africa rainfed conditions. Nonetheless, boll opening should not happen before the end of the rainy season since cotton could fall on the ground or suffer from bacteria and fungi attacks affecting fiber quality (Buxton et al., 1973). If the anthesis comes early, reproductive duration should be proportionally longer. On the contrary, if anthesis date remains unchanged, reproductive duration cannot be extended too much to prevent a risk of end of rainy season before the cut out. Additionally, in Northern Cameroon, the socioeconomic context led to an increasing proportion of farmers planting late (Cao et al., 2011). In these conditions, Sekloka et al. (2007) observed delayed first-flower opening, accelerated last-boll development and reduced effective flowering time. This confirms the urge for adapting cotton to sub-optimal conditions as an alternative to current cultivars.

This study found at least two ideotypes candidates. When compared to the cultivar L484, the two candidate ideotypes (L484_25 and L484_24) showed some interaction with cropping conditions on seed cotton yield (Figure 32). In the best cropping conditions (North on station with higher soil fertility, depth and longer rainy season pattern), the current cultivar L484 performed better than ideotype candidates. On the other hand, in the worst conditions, L484 yielded less than the two other VC. This was not surprising since plant breeding has always been performed in the best rainfed conditions and targeted cultivars with high yield potential (Dessauw and Hau, 2007) rather than resilient ones. Jeuffroy et al. (2014) reviewed the use of CSM to represent the interaction between genotypes, environments and management (G x E x M). They highlighted that CSM could represent them and should be useful for cultivar assessment, or in the definition of crop management adapted to cultivars, and even to support breeding programs. Similarly, we found that CROPGRO-Cotton was able to represent G x E x M (Figure 32). Suriharn et al. (2011) also found that CROPGRO-Peanut (very close to CROPGRO-Cotton) was able to represent these interactions as it was successful in the design of crop ideotype for target environments. Design of ideotype by simulation might be a complementary cornerstone into crop breeding for suboptimal environments. Webber et al. (2014) reviewed that CSM in Sub Saharan Africa could be helpful for food security achievement, facing low soil fertility and climate change and variability. In Cameroon, the experimental costs to get the minimum dataset necessary for CSM calibration and validation corresponded to less than two years of plant breeding. Nonetheless, ideotypes are plant models;

best combination of traits might not exist yet as a cultivar and might not even be created. Creating these corresponding cultivars take several years and further evaluation of actual performance has to be performed. In addition some genetic parameters have correlated values in the real world; for example, ideotype with both thinner leaves and more photosynthetic capability might only exist if the cultivar has a faster phyllochron or shorter green leaf area duration (faster leaf turnover). User should be careful of the significance of genetic parameters combination.

4.3. Limitations of the study

We performed a sensitivity analysis on a subset of genetic parameters while a wider set of genetic parameters could have resulted in other ideotypes which might be even more suitable. Using both local and global sensitivity analyses, Pathak et al. (2007) showed that SLAVR, KCAN and SD-PM were the genetic parameters of cultivars affecting the model output (yield and crop cycle length) the most. In this work SLAVR and SD-PM were used in addition to other parameters. However, further study of the light extinction coefficient should be included.

One limit of this work is that, working on research stations as in Sanguéré, we obtained much higher yields than in farmers' fields which are usually about 1200 kg ha^{-1}. Further studies done on farms aiming at estimating and modelling the impact of additional processes related to other constraints experienced by farmers which are thoroughly represented by the model yet should help providing even more suitable ideotypes. These processes are usually called the reducing factors (van Ittersum et al., 2003). For example, the model does not represent the impact on the soil water and nutrient resources available to the crop of all weeds present in northern Cameroon, while farmer weeding capacity is often found to be sub-optimal since labor limited. Another limitation of the model is its representation of roots which is very simplistic; there are no cultivar or ecotype level root genetic parameters in DSSAT CROPGRO-Cotton. York et al. (2013) demonstrated that root phenes characterization is very likely to be an efficient way to optimize soil resource acquisition and should be of great help in the breeding of crops with superior stress tolerance and reduced dependence on intensive use of inputs.

4.4. Importing crop physiology into breeding activities: which additional measurements?

In the phase F5 of the breeding program, for each line, calculating the ratio of the "duration from emergence to anthesis" to the "duration from emergence to 1st open boll" should be relevant. We recommend selecting cultivars with a low ratio. In addition, simple measurements of chlorophyll content and leaf thickness could help improving the efficiency of breeding programs. It could be easily implemented around time of anthesis. In order to measure specific leaf weight (SLW), 10 disks of leaves should be sampled on each line of the F5 with a leaf disk sampler bigger than the one described by Wullschleger and Oosterhuis (1986). The surface sampled on each disc should be about 10 cm² (example of leaf disc sampling: http://www.redebel.be/en/fields-trials/residue-trials/sampling-residue.html). Then, the dry weight of samples should be measured after 2 days of oven drying at 80°C or even sun drying if no oven available. For example, sampling one leaf on the main stem from the mid-height of the plant on 10 plants in the line would be recommended. In order to provide chlorophyll content, SPAD measurements can be performed on the same leaves next to sampling. This measurement should be more time consuming than leaf sampling and several SPAD-meters should be used as measurements might take about 1 min per line. Lines where heavy sample weights and high SPAD values are found should be selected. These additional measurements should only slightly increase the cost of the breeding program; they can be performed by two to three technicians within a couple of days (plus drying and weighting). Precision scales (10^{-3} g) should be used; they are usually available on research stations.

5. Conclusion

We studied the capability of CSM to design African rainfed cotton ideotypes. The model DSSAT CROPGRO-Cotton successfully represented the interactions between cultivars and cropping conditions on seed cotton yield. It should be used along with regular breeding methods to increase breeding efficiency (timing and level of improvement). The ideotype found by simulation had a shortened emergence to anthesis duration with increased reproductive duration (same total cycle length), higher photosynthesis potential and thicker leaves. The leaf maximum size was not consistent. These ideotypes should be targeted and cultivars alike should be used when length of rainy season is expected to be short because of late planting due to higher priority given to food crops or simply to later onset of rainy season.

This crop model demonstrated a good potential for cotton breeding support in African rainfed conditions but it will have to be coupled with a model of cotton fiber quality since a high yield along with bad fiber quality is not optimized economically. Coupling should be possible since successful examples of model coupling have been documented on sunflower (Andrianasolo et al., 2014) and some quality model are already in use for cotton (Zhao et al., 2012).

Final discussion

The seed cotton yield in Northern Cameroon has been declining for the last thirty years (Naudin et al., 2010). The genetic part of this decline has not yet been well understood.

The study tackled the following questions:

- Do recent cultivars have adaptation traits to the cotton production area in Cameroon?
- Does the CSM represent GEI under water limited conditions?
- Which are the characteristics of rainfed cotton ideotypes in Cameroon?

To answer these questions:

We evaluated and analyzed the genetic improvement of yield and fiber quality of widely cultivated Cameroonian cotton cultivars to determine whether this genetic improvement was affected by the planting date and water availability conditions (chapter 1).

Then, we focused on the effect of water deficit conditions on plant morpho-physiological traits on a subset of four cotton cultivars (chapter 2).

Using both field and greenhouse experiments, we reproduced a wide range of water deficit conditions from "no deficit" to "intense water deficit from the very beginning of the crop cycle." Finally, based on the previous observations, we calibrated, validated, and used a crop simulation model (DSSAT CROPGRO-Cotton) (chapter 3).

We evaluated two cultivars and 42 virtual cultivars on 99 generated climates in two locations with different rainy season patterns. We selected the two best virtual cultivars on average across the locations and climates and re-evaluated them in actual measured conditions of 2012 and compared them to cultivar L484 still cultivated (chapter 3).

1. Do recent cultivars have adaptation traits to the cotton production area in Cameroon?

In Cameroon, breeding efforts have successfully increased the cotton fiber yield (3.3 kg ha^{-1} $year^{-1}$) via an increase in fiber percentage (3.9 to 6.2 % in 60 years). Cameroonian cotton fibers are of good quality, and breeding efforts increased their length, uniformity, strength, and standard fineness potentials. The increase in fiber yield by breeding efforts was exclusively due to increase in fiber percentage. However, neither other yield components, nor aerial biomass production and harvest index have been changed by breeding efforts. Consequently, in all our field experiments, we found no improvement in seed cotton yield. The absence of cotton yield components and yield improvements was likely due to three main reasons. Firstly, despite breeding efforts, there was no evolution of crop cycle duration. Secondly, recently bred cotton plants showed the same physiological functioning: leaf thickness at the beginning of anthesis, stomatal conductance, net photosynthesis, and radiation use efficiency were not significantly different from older cultivars. Thirdly, plant vigor and root properties of recent cultivars were decreased compared to ancient ones at a very early stage of development, and there was no improvement of water or nutrient uptake. In conclusion, breeding efforts did not improve plant efficiency for light interception, light use, and nutrient and water uptake. However, breeders have succeeded in creating cultivars with the characteristics that the development company asked for since they increased the percentage of fiber, the fiber yield, and the potential of fiber quality.

The genetic improvement for cotton fiber yield was smaller than that observed (S. M. Liu et al., 2013; Rochester and Constable, 2015; Schwartz and Smith, 2008a)). This was probably because breeding in Cameroon was focusing on increasing potential production rather than adaptation to local unfavorable growing conditions (poor soil fertility, harsh climate, no irrigation). Nonetheless, since soils in northern Cameroon show high spatial variability of soil fertility, working with the best practices (fertilization, weeding etc.) combined with ploughing allowed breeders to compare plants in relatively higher homogeneous conditions compared to the expected.

Similarly to Hsiao (1973), experienced water deficit had a negative impact on almost all the plant functions, both under field and controlled environments. Despite non-significant interaction between soil water availability and cultivars on most variables, recently released cultivar bred for the Far North region (L484), displayed the greatest photosynthetic activity, level of transpiration, and crop development in sub-optimal conditions. In water deficit conditions, L484 had thicker leaves with more chlorophyll than older cultivars which is a characteristic of drought resistance

(Jagmail Singh et al., 1990). Therefore, L484 maintained higher instant net photosynthesis in drought conditions compared to older cultivars leading to a smaller relative reduction of RUE of L484 compared to the older ones. L484 also maintained relatively high WUE and transpiration. Cultivar L484 seemed to follow a strategy of growth maintenance however it did not show any enhancement of seed cotton yield, especially in drought conditions.

We concluded that there was no trend of adaptation to drought conditions as a response of breeding efforts. However, breeders provided a cultivar (L484) which seemed to be better adapted to drought conditions, especially in case of early season droughts.

2. Does the CSM represent GEI under water limited conditions?

The interaction between genetic improvement and cropping conditions was only significant for some fiber quality parameters. Under water constraint, in this study, the quality of cotton fibers was reduced despite breeding efforts. There was no cropping condition (environment, management) by genetic improvement rate interaction on radiation use, development and growth, biomass, and yield variables. Similarly, no cropping condition by cultivar interaction was found on water use and previously listed variables. This result was surprising since breeding selected best plants in rainfed drought-prone conditions, and yet we expected a better adaptation to drought conditions of recently released cultivars compared to ancient ones. It suggests that these cultivars are pretty alike. Consequently, crop performance is highly dependent on non-controllable environment, and it might simply follow climatic variability.

In our study, few GEI were observed, and principally on variables not simulated by DSSAT CROPGRO-Cotton. Nonetheless, the CSM DSSAT CROPGRO-Cotton reproduced pretty well the patterns observed in campo for cultivars AC and L484 as both cultivars' genetic parameters were representative of their observed traits. Cultivar L484 was represented with smaller and thicker leaves, and higher resilience in drought conditions compared to AC. Initial simulations confirmed the absence of differences on seed cotton yield between cultivar AC and L484, whatever the cropping conditions.

We concluded that the model is likely to represent GEI. It did represent well the behavior of two existing cultivars and was capable of simulating GEI on yield using existing cultivar L484 and two ideotypes for rainfed conditions. However, most of the GEI observed in campo in this study were linked to lint quality and no description of quality is provided by DSSAT CROPGRO-Cotton.

Consequently, further study should be done using very different genotypes to confirm whether the model still represent GEI.

3. Which are the characteristics of rainfed cotton ideotypes in Cameroon?

In order to identify cultivars with potentially higher yields, on average, in rainfed conditions, forty-two virtual cultivars (VC) were compared to the L484 in a large variability of climates representative of North and Far North regions of Cameroon. Both in the North and the Far North region, the best candidate for ideotype had earlier anthesis date, longer reproductive duration, thicker leaves with higher potential assimilation rate compared to the reference cultivar L484. In the North region, on average over the 99 years, it was suggested by the simulations that having bigger full size leaf compared to L484 should be favorable whereas in the Far North it was the opposite. However, these cultivars should not perform better than L484 in the best conditions.

We concluded that both cultivars with relatively high potential like the one successfully bred (L484) and with high resilience (ideotypes) should be available to famers. Thus, they will be able to adjust their choice on the amount of resource available (how much fertilizer they are willing to use, whether they are able to plant as early as the rainy season onset, etc.). If they are resourceful and the rainy season starts early, they should go for L484-like cultivar, otherwise for ideotype-like cultivar.

4. Limitations of the study

This experimental study was based only on two years and two locations; the different crop management systems compensated partly the limited size of the network. As a result, we could only observe a small part of the existing climatic variability. Similarly, the cotton cultivars used gave a fair representation of genetic variability in Cameroon (necessary for genetic gain evaluation) but a very limited part of existing genetic variability of cotton (okra leaf, determinate, with small vegetative development, genetically modified, etc.). In addition, all cultivars were cultivated under the same crop management, not necessarily the ones used when they were widely cultivated in Cameroon. This was especially true for the first two cultivars, AC and NKOUR, originally cultivated without fertilizer or pesticides. The greenhouse experiment with water limiting conditions was not carried out until harvest. Snowden et al. (2014) showed that timing of stress event is critical for cotton yield as in most other crops. However, such an early and high level of water-limited conditions would have probably led to almost no yield. The candidates for Cameroonian rainfed

cotton ideotype were designed with a subset of five genetic parameters to which a fluctuation of ±20 % was applied compared to the reference level. A bigger set of genetic parameters with more levels for each parameter could have led to other ideotypes which might have been more suitable. Nonetheless, Pathak et al. (2007) performed a global sensitivity analysis of the CSM and found that (i) the specific leaf area under standard growth conditions (SLAVR) was the most important model parameter influencing cotton yield under both irrigated and rainfed conditions when taking into account its range of uncertainty, and (ii) the duration between first seed and physiological maturity (SD-PM) was the most important parameter for season length response. Design of ideotype by simulation might be a complementary cornerstone into crop breeding for suboptimal environments. Webber et al. (2014) reviewed that CSM in Sub Saharan Africa could be helpful for food security achievement, facing low soil fertility and climate change and variability. Nonetheless, it is necessary to verify if cultivar ideotype-like performs better than existing cultivars in poor rainfall conditions.

5. Perspectives

5.1. Importing crop physiology into breeding activities: which additional measurements?

Cotton breeding strategy is not fully optimized for seed cotton yield improvement in rainfed northern Cameroon conditions. In order to breed for drought resistance, breeding should be performed in drought conditions. However this is not a suitable option due to importance of heterogeneity. A major shift in the ranking of breeding criteria is needed. Some physiological variables related to yield in water-limited conditions should be identified and targeted since some variables have already been demonstrated successfully e.g. metabolic response on peanut (Singh et al., 2014); greater RUE at the canopy level and high leaf assimilation rate on cereals (Fischer and Edmeades, 2010); leaf enhanced ribulose bisphosphate carboxylase activity on cotton (Plaut and Federman, 1991). Targeting ecophysiological traits should provide proxies allowing the evaluation of cultivar performance in many more conditions than ones actually experienced in campo.

According to our results, both in the North and the Far North region, the best candidate for ideotype had earlier anthesis date, longer reproductive duration, thicker leaves with higher potential assimilation rate compared to the reference cultivar L484. In the North region, on average over the 99 years, it was suggested by the simulations that having bigger full size leaf compared to L484 should be favorable whereas in the Far North it was the opposite. Targeting

these ideotype-like cultivars implies additional measurements. Which measurements can be easily implemented in the breeding processes?

The first four years (generations F1 to F4) of a breeding sequence, only single plants are selected. This is when the highest genetic variability exists but, no measurement can be done easily on every single plant. Conversely, on generation F5, breeders select a full line (10 m long) and physiological traits can begin to be evaluated. During the next steps, genetic variability is drastically reduced. Indeed, due to limited plots areas, only a few lines can be selected and compared on bigger plots. During the cotton breeding cropping season, there are several bottlenecks where most technicians are required for the management of the labor force. During these periods, any supplementary measurement is not appropriate. This is especially true for planting, a few weeks after beginning of flowering, and harvesting.

Considering all these constraints, we recommend to implement measurement of physiological traits as early as in generation F5 where there are still many different lines and already a population of plants. For each line, calculating the ratio of the "duration from emergence to anthesis" to the "duration from emergence to 1st open boll" should be relevant. These phenologic measurements are well known and already done extensively for breeding steps found the years after F5. A technician should sum up all white flowers blooming on a line and when this number adds up to half the number of plants in the line, anthesis can be counted. Within an hour, one technician alone can count more than 100 lines. Similar methodology should be followed for open bolls. We recommend selecting cultivars with low ratio.

In addition, simple measurements of chlorophyll content and leaf thickness could help improving the efficiency of breeding programs. It could be easily implemented slightly before anthesis while labor demand is low. In order to measure specific leaf weight (SLW), 10 disks of leaves should be sampled on each line of the F5 with a leaf disk sampler bigger than the one described by Wullschleger and Oosterhuis (1986). The surface sampled on each disc should be about 10 cm^2. Then, the dry weight of samples should be measured after 2 days of oven drying at 80°C or even sun drying if no oven available. For example, sampling one leaf on the main stem from the mid-height of the plant on 10 plants in the line would be recommended. In order to provide chlorophyll content, SPAD measurements can be performed on the same leaves next to sampling. This measurement should be more time consuming than leaf sampling and several SPAD-meters should be used as measurements might take about 1 min per line. Lines where heavy sample weights and high SPAD values are found should be selected. These additional measurements

should only slightly increase the cost of the breeding program; they can be performed by two to three technicians within a couple of days (plus drying and weighting). Precision scales (10^{-3} g) should be used; they are usually available on research stations.

5.2. Using and improving the production model

In Cameroon, CSM calibration and validation costs correspond to less than two years of plant breeding, after that step, in silico experiments are free. Nonetheless, ideotypes are plant models; best trait combination might not exist yet as a cultivar and might not even be feasible. Creating these corresponding cultivars take several years and further evaluation of actual performance has to be performed. In addition some genetic parameters have correlated values in the real world which are not represented in the model; for example, ideotype with both thinner leaves and more photosynthetic capability might only exist if the cultivar has a faster phyllochron or shorter green leaf duration (faster leaf turnover). Users should be careful of the significance of genetic parameters combination.

The model representation of roots is very simplistic; there are no cultivar or ecotype level root genetic parameters in DSSAT CROPGRO-Cotton. York et al. (2013) demonstrated that root phenes characterization is very likely to be an efficient way to optimize soil resource acquisition and should be of great help in the breeding of crops with superior stress tolerance and reduced dependence on intensive use of inputs. Additionally, soil is represented in one dimension only, the spatial representation of roots architecture is not accurate, especially the potential root extraction on a perpendicular axis to the line, it should be represented in 2D if not 3D.

The identification and evaluation of the impact of reducing factors (van Ittersum et al., 2003) found in northern Cameroon should be performed. This will provide inputs for the modelling of additional processes. For example, since weeding is labor intensive, the impact of main weeds found in Cameroon on the soil water and nutrient resources available to the crop should be modeled.

Finally, the use of genetically modified cotton crop is increasing. However, DSSAT CSM cannot formally simulate the impact of these cultivars versus their corresponding wild-type. For example, the fitness costs of the technology for the plant, impact on biotic stress, reduction of transpiration, etc. Further study combining both wild-type and corresponding GMO should be done in order to model underlying processes.

5.3. Coupling the model of production with a model of quality

We found that DSSAT CROPGRO-Cotton demonstrated a good potential for cotton breeding support in rainfed conditions in Cameroon. However, this CSM focused on increasing cotton quantity, and yet cotton is also evaluated for its quality. Indeed, high yield along with bad fiber quality does not optimize economic return. We do not know yet if ideotypes selected according to our physiological traits will maintain high fiber quality. Consequently, we invite breeders to carry on their evaluation on fiber quality in addition to our recommendations until we successfully couple our model with a model of cotton fiber quality, like those developed by Zhao et al. (2013) or Wang et al. (2014). Coupling should be possible since successful examples have been documented on sunflower (Andrianasolo et al., 2014) and some quality models are already used for cotton (Zhao et al., 2012). Coupled models will also have to model pest impact on fiber quality, which should be feasible, as this was already implemented for some pests on cotton production (Ortiz et al., 2009).

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Appendixes

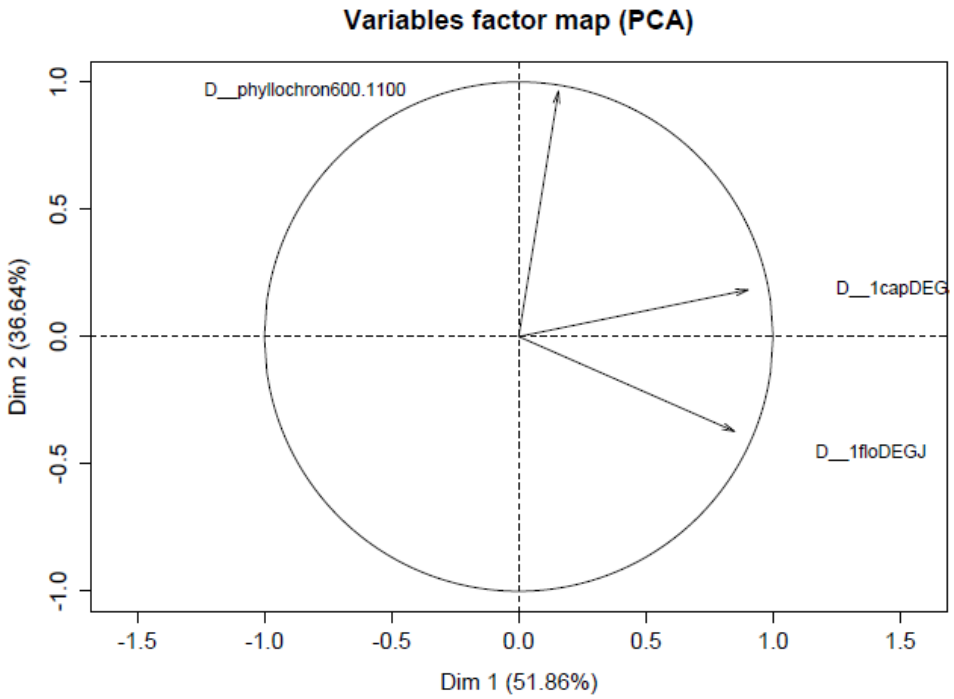
Appendix 1. Range of means (adjusted) across cultivar by cropping condition for each variable.

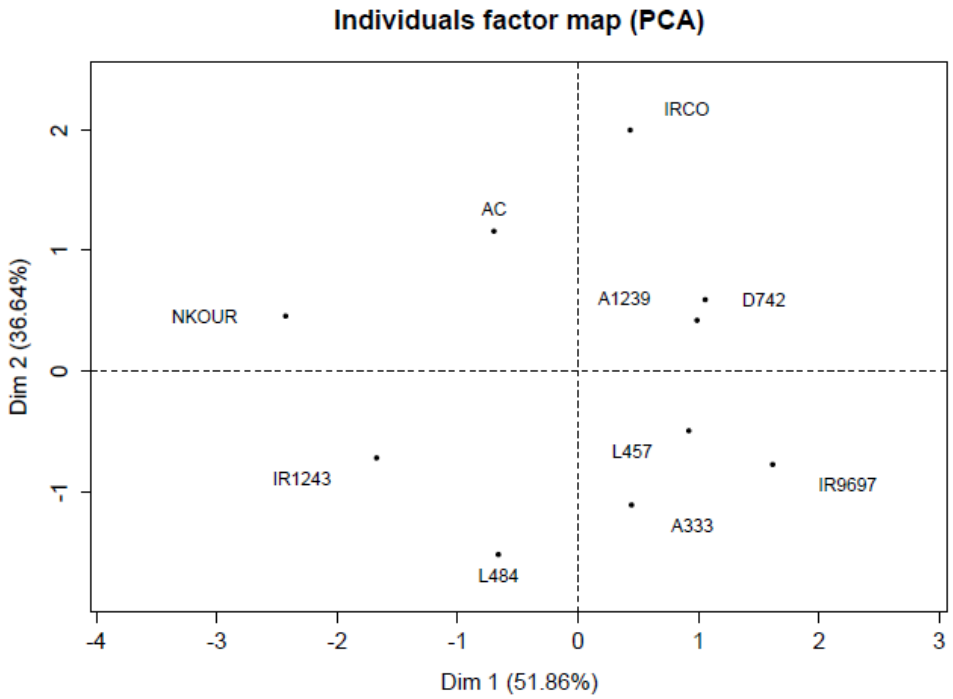
Variables	Unit	Garoua G0		Garoua G1		Garoua G2		Maroua		Greenhouse	
		Means	S.E.	Means	S.E.	Means	S.E.	Means	S.E.	Means	S.E.
Yield and components											
Ginning out-turn	[%]	39.8	0.2	40.1	0.2	38.7	0.2	37.8	0.6	-	-
Boll number per meter square	[nb m^{-2}]	54.1	4.0	49.9	4.0	32.7	4.0	23.4	0.7	-	-
Average boll weight	[g]	5.3	0.2	5.2	0.2	4.0	0.2	-	-	-	-
Seed cotton yield	[kg ha^{-1}]	2770	203	2408	203	1357	203	1139	32	-	-
Fiber Yield	[kg ha^{-1}]	1105	83	965	83	542	83	457	16	-	-
Seed mass index	[g/100 seeds]	9.4	0.2	8.8	0.2	8.2	0.2	9.1	0.1	-	-
Fiber quality											
Yellowness index (+b)	[%]	9.3	0.1	9.0	0.1	9.0	0.1	10.9	0.1	8.5	0.1
Elongation	[%]	6.9	0.1	6.5	0.1	6.6	0.1	5.7	0.1	6.0	0.1
Fineness standard (HS)	[mtex]	201	5	201	5	199	5	202	3	189	4
Micronaire index (IM)	-	3.7	0.1	3.6	0.1	3.7	0.1	3.7	0.0	4.0	0.1
Maturity ratio (MR)	[%]	82.4	2.0	80.5	2.0	82.8	2.0	81.3	0.8	89.1	1.6
Brightness (Rd)	[%]	79.6	0.2	79.5	0.2	79.9	0.2	77.7	0.2	79.6	0.2
Short fiber index (SFI)	[%]	6.8	0.1	7.1	0.1	6.9	0.1	7.4	0.1	-	-
Strength	[g tex^{-1}]	31.0	0.8	31.0	0.8	32.1	0.8	31.2	0.2	31.6	0.5
Upper half mean length (UHML)	[mm]	29.3	0.3	29.4	0.3	29.8	0.3	28.2	0.2	31.0	0.4
Uniformity index (UI)	[%]	84.4	0.2	84.0	0.2	84.4	0.2	83.5	0.1	85.8	0.2
Development & Growth											
Duration from emergence to anthesis	[†GDD]	915	17	842	17	831	17	1043	6	-	-
Duration from emergence to 1st open boll	[GDD]	1627	13	1536	13	1475	13	1685	8	-	-
Main stem height	[cm]	120	8	120	8	89	8	119	2	-	-
Number of vegetative branches	-	2.1	0.3	2.5	0.3	2.0	0.3	2.0	0.1	-	-
Number of leaves at 65 DAP	-	59.7	5.5	55.9	5.5	42.2	5.5	41.1	1.6	-	-
Max nb of node on main stem	-	25.1	0.5	22.9	0.5	21.0	0.5	21.1	0.2	-	-
Node of insertion of 1st fruiting branch	-	6.7	0.1	6.3	0.1	6.4	0.1	6.6	0.1	-	-
Early phyllochron	[GDD $node^{-1}$]	-	-	-	-	-	-	-	-	43.1	0.4
Late phyllochron	[GDD $node^{-1}$]	48.5	1.3	54.7	1.4	48.4	1.3	50.9	0.3	130.4	4.6
Radiation Use											
Carbon assimilation rate	[µmol CO2 m^{-2} s^{-1}]	-	-	-	-	-	-	-	-	17.3	0.4
Stomatal conductance	[mmol H2O m^{-2} s^{-1}]	-	-	-	-	-	-	-	-	267.5	7.6
Leaf area index (LAI) at 65DAP	-	1.5	0.3	1.7	0.3	1.1	0.3	2.1	0.1	-	-
LAI at maximum vegetative stage	-	2.9	0.3	3.1	0.3	-	-	2.9	0.1	-	-
Leaf pilosity	-	0.8	0.1	1.1	0.1	1.3	0.1	1.1	0.1	-	-
Radiation use efficiency	[g dry biomass MJ^{-1}]	1.3	0.1	1.9	0.1	1.1	0.1	1.3	0.0	-	-
Specific leaf area at 65 DAP	[cm^2 g^{-1}]	285	22	163	22	161	22	166	8	247	5
1 leaf average area at 65 DAP	[cm^2]	76.9	4.9	77.8	4.9	59.1	4.9	78.2	1.4	-	-
Biomass and allocation											
Aerial dry biomass at 120 DAP	[kg ha^{-1}]	7795	567	6174	567	4423	581	5189	253	-	-
Harvest index	[%]	38.9	3.1	41.2	3.1	31.6	3.2	24.1	1.4	-	-

Appendix 2. Methodology for the subset of cultivars.

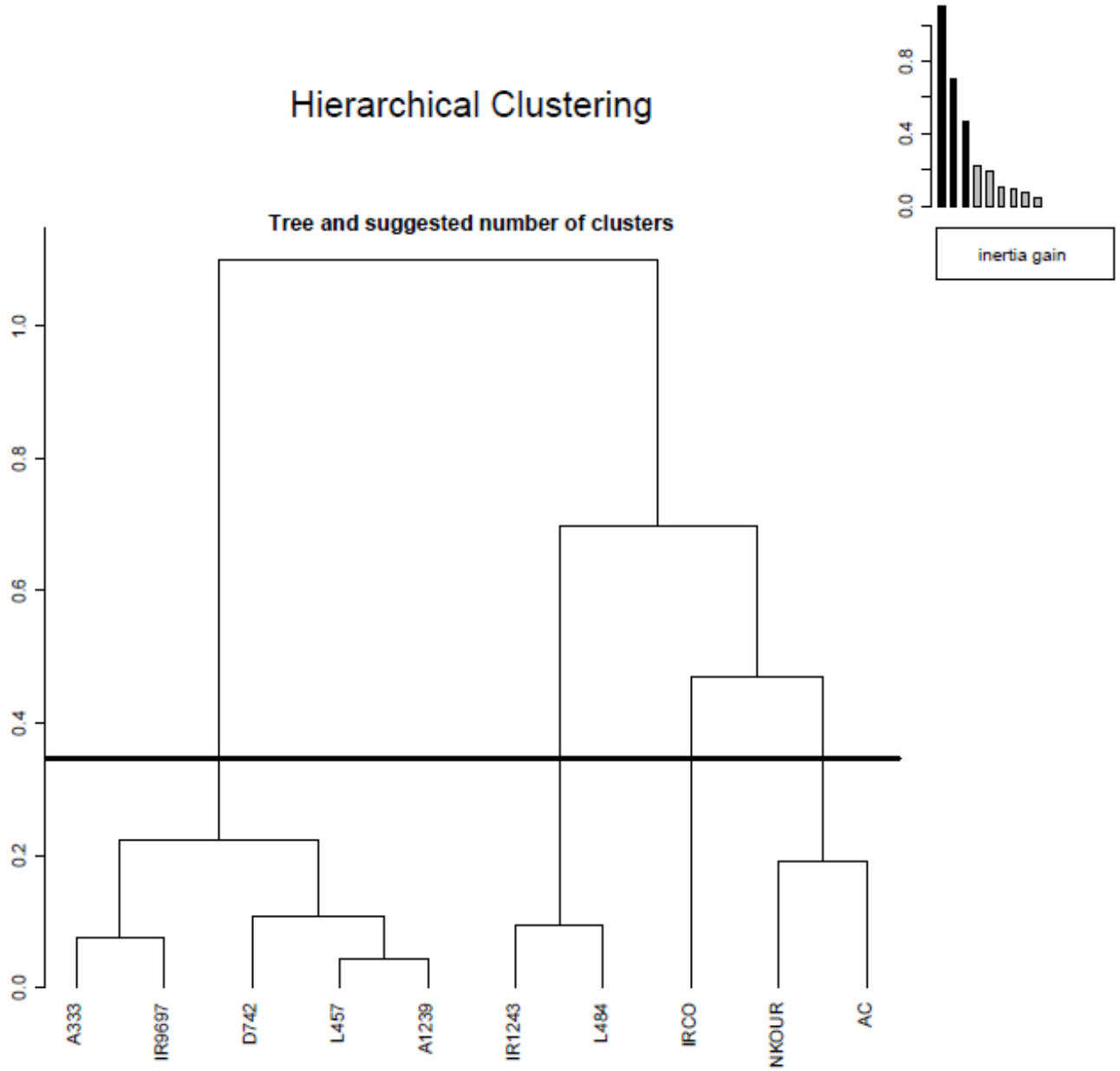
For each group of variables, principal component analyses (PCA) were performed on averaged values per cultivar across cropping conditions (G0, G1, G2, and M0) using {FacotMineR} package (Lê et al., 2008). Missing values were replaced according to an algorithm in the package {missMDA} (Josse and Husson, 2012). Clustering was done on outputs of PCA. Number of cluster was adjusted according to the amount of inertia lost if only one group was considered instead of two. Development / Three main variables characterizing cotton development were used: duration in growing degree days (GDD, base 13°C) from emergence to anthesis (D__1floDEGJ), from emergence to physiological maturity (1st open boll: D__1capDEGJ), and the phyllochron between 600 and 1100 GDD (D__phyllochron600.1100). The first 2 components represented 88.5% of the variability observed (S1 Figure). The first component represented duration, positive value for longer cycles. NKOUR and IR1243 had the shortest cycle whereas IR9697 and D742, the longest. The second component represented the phyllochron, positive value for slower development. IRCO and AC had the slowest node emission whereas L484 and A333 had the fastest. A hierarchical clustering analysis found four different groups (S2 Figure). Cultivars A333, IR9697, D742, L457, and A1239 belonged to the same cluster. Cultivars IR1243 and L484 were also clustered. Cultivar IRCO was alone in its cluster. Finally, NKOUR and AC were clustered. Morphology / Four variables characterized the plant morphology. These variables were the number of vegetative branches (M__NbBV), the maximal number of node on the main stem (M__NdNdmax), the final plant main stem height (M__Hautm), and the node of insertion of the first fruiting branch on the main stem (M__Nd1BF). The first 2 components represented 79.1% of the variability observed (S3 Figure). The first component represented the hierarchical clustering analysis found four different groups (S4 Figure). Cultivars IRCO, NKOUR, and D742 belonged to the same cluster. Cultivars IR9697, A333 and AC were also clustered. Cultivar L484 was alone in its cluster. Finally, A1239, L457 and IR1243 were clustered. Choice of cultivars / The cultivars IRCO and L484 were selected as they were different from other cultivars for development and morphology variables, respectively. As a consequence, the other cultivars sharing clusters with these two cultivars were withdrawn from the potentially selected cultivars; cultivar IR1243 was removed (development) and, NKOUR and D742 were also removed (morphology). Cultivar AC was then selected, as the only cultivar in its development variables cluster after NKOUR removal. Consequently, IR9697 and A333 were removed from list of cultivar. One more cultivar had to be selected to represent the last cluster both in development and morphology groups. This cultivar was either A1239 or L457. We selected L457 as it is still cultivated and replaced

S1 Figure. Principal component analysis on development variables. On the left, contribution of variables on the first two components. On the right, contribution of cultivars on the first two components.

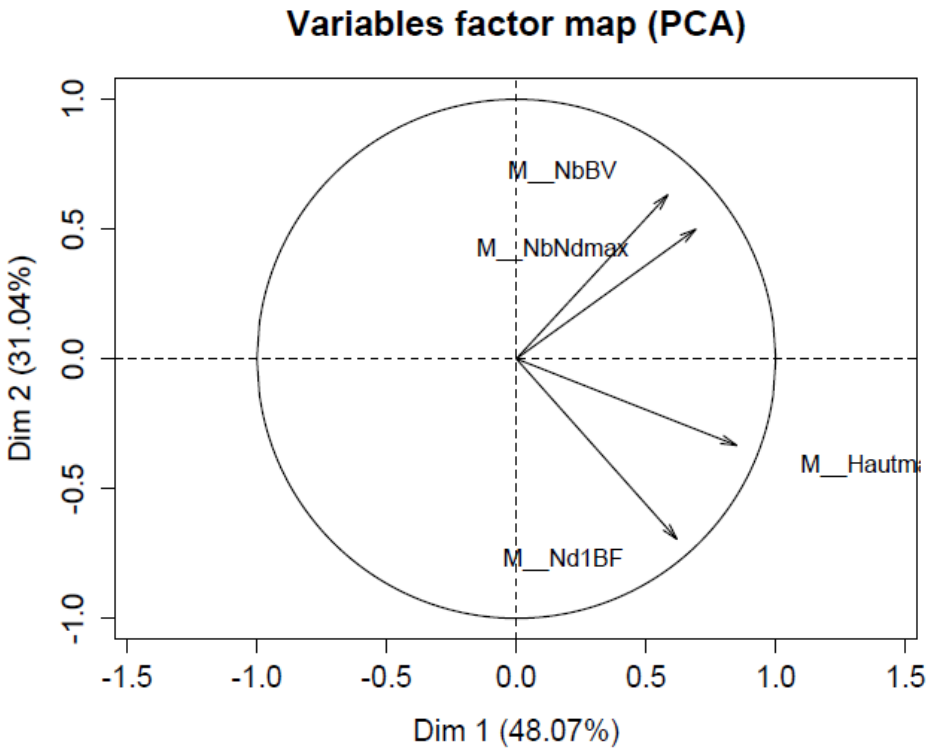


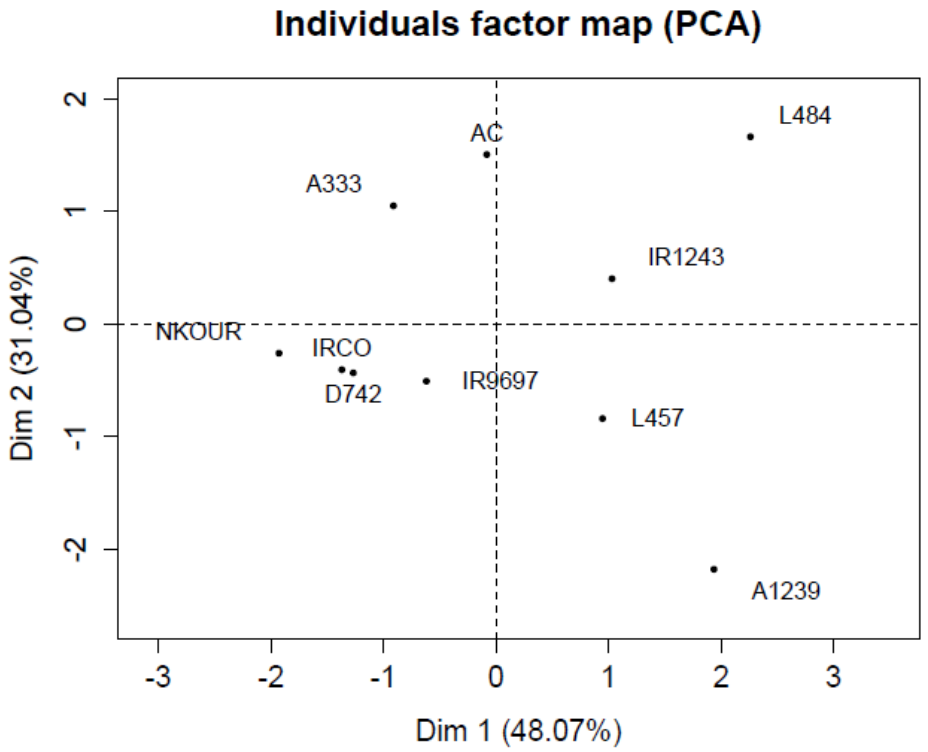


S2 Figure. Hierarchical clustering on development variables. Four clusters were found on development variables.

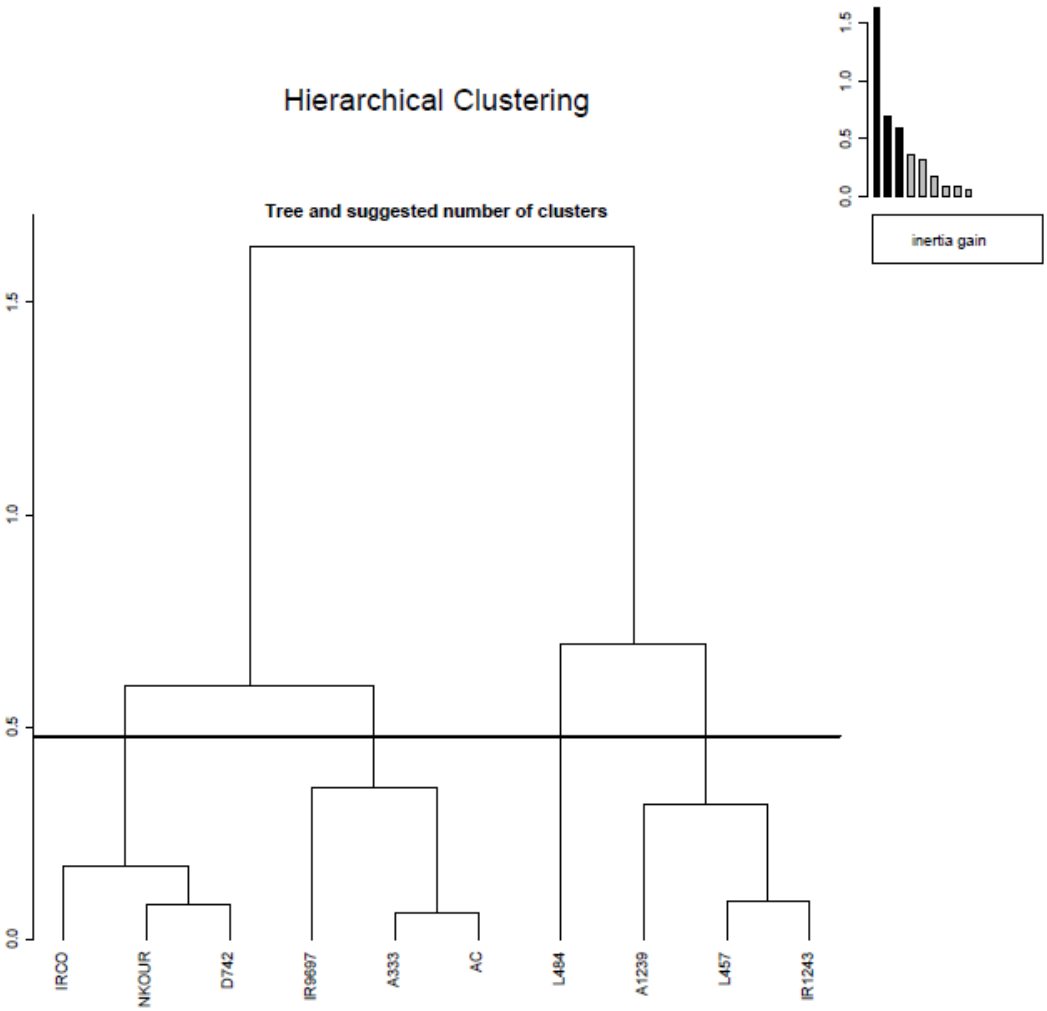


S3 Figure. Principal component analysis on morphology variables. On the left, contribution of variables on the first two components. On the right, contribution of cultivars on the first two components.

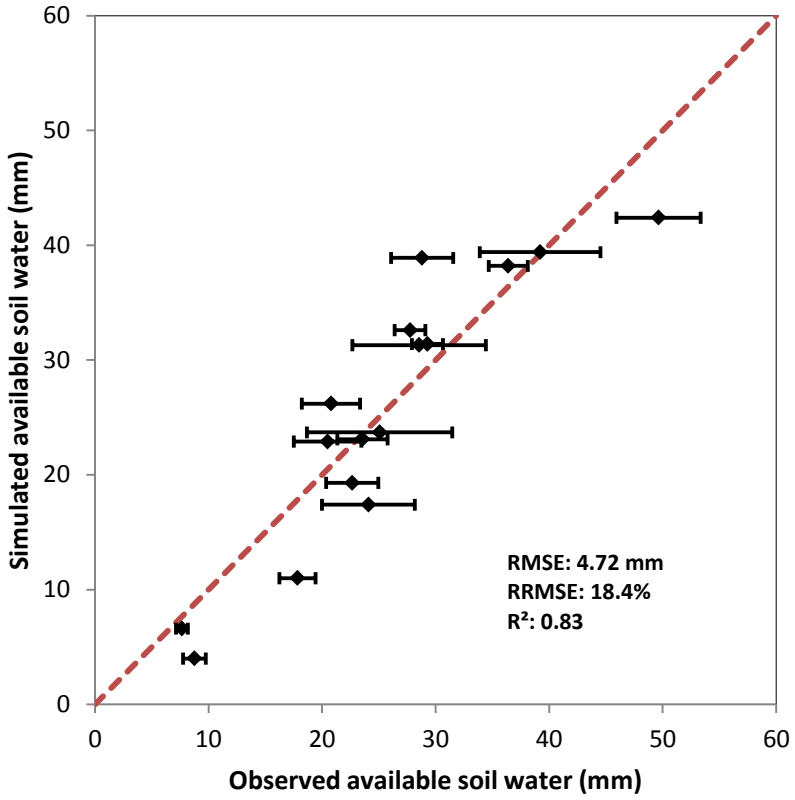




S4 Figure. Hierarchical clustering on morphology variables. Four clusters were found on morphology variables.



Appendix 3. Available soil water content observed and simulated by PROBE-W (mm) in the experiment of Sanguéré in 2013.



Horizontal bar indicates 5 % confidence interval.
The dashed line represents the y=x curve.
RMSE: root mean square error;
RRMSE: relative root mean square error;
R^2: coefficient of determination.